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## Alcheringa: An Australasian Journal of Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/talc20>

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Published online: 10 Dec 2013.

To cite this article: Mercedes B. Prámparo, Alberto L. Cione & Bernardo Gonzalez Riga , Alcheringa: An Australasian Journal of Palaeontology (2013): Sharks (Neoselachii) and palynomorphs from Mendoza (Argentina): new evidence of the Late Cretaceous Atlantic marine transgression, Alcheringa: An Australasian Journal of Palaeontology, DOI: [10.1080/03115518.2014.849027](https://doi.org/10.1080/03115518.2014.849027)

To link to this article: <http://dx.doi.org/10.1080/03115518.2014.849027>

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# Sharks (Neoselachii) and palynomorphs from Mendoza (Argentina): new evidence of the Late Cretaceous Atlantic marine transgression

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PRÁMPARO, M.B., CIONE, A.L. & GONZALEZ RIGA, B., 2013. Sharks (Neoselachii) and palynomorphs from Mendoza (Argentina): new evidence of the Late Cretaceous Atlantic marine transgression. *Alcheringa* 38, 000–000. ISSN 0311–5518.

Neoselachian (modern shark) teeth and palynomorphs have been recovered from the Late Cretaceous Jagüel Formation in the Province of Mendoza, Argentina. The fossiliferous beds were deposited during the Atlantic transgression that covered northern Patagonia and other parts of South America from the Maastrichtian to the Danian. Teeth of several lamniform sharks are attributed to the anacoracid *Squalicorax pristodontus* and cf. *Serratolamna serrata* of indeterminate familial affinity. These taxa became extinct at the end of the Cretaceous and confirm the late Maastrichtian age previously assigned to the Jagüel Formation in this northwestern part of the Neuquén Basin. For the first time, the selachian faunas are described together with algae and dispersed organic matter assemblages (palynofacies), revealing new elements of the neritic biota leading up to the Cretaceous–Paleogene (K–Pg) mass extinction in South America. The palynoflora consists exclusively of the prasinophyte algae *Tasmanites*, *Cymatiosphaera* and *Pterospirmella*, indicative of stratified saline waters. Dispersed organic components in the profile (mainly opaque equidimensional phytoclasts and prasinophytes) are consistent with an inner neritic environment, with evidence (a great variety of particle sizes, lath-shaped phytoclasts increasing slightly in number and decreasing number of marine components) of slightly more nearshore conditions towards the upper part of the profile. These marine biotas confirm the presence of an epeiric sea over northern Patagonia, which extended westwards to the volcanic arc on the western flank of the Andean Cordillera in Mendoza.

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Key words: Neoselachii, shark teeth, Prasinophytes, organic matter assemblages, Late Cretaceous, southern Mendoza, Argentina.

SEVERAL Upper Cretaceous units are exposed in Mendoza Province with evidence of intermittent marine environments within the Malargüe Group (Loncoche, Jagüel and Roca formations). These strata were deposited during the maximum advance of the Atlantic Ocean during the final phase of the Cretaceous and Early Paleogene.

The Late Cretaceous saw extensive radiation within several marine vertebrate clades. Unfortunately, South American Late Cretaceous marine fishes are poorly known in comparison to coeval ichthyofaunas from North America and Europe (Cappetta 2012). In particular, such faunas are extremely rare in Argentina (see Arratia & Cione 1996, López Arbarello *et al.* 2003, Bogan & Agnolin 2010, Bogan & Gallina 2011). Several sharks became extinct during the biotic crisis at the end of the Cretaceous (Shimada & Brereton 2007). Consequently, they are useful for stratigraphic demarcation of the Cretaceous–Paleogene (K–Pg) boundary.

The marine palynomorphs of the Malargüe Group are poorly documented (Papú *et al.* 1999, Prámparo &

Papú 2006). Previously, palynomorphs of the Jagüel Formation in the northwestern sector of the Neuquén Basin were known only from the Cerro Butaló section (Prámparo & Papú 2006).

Here, we describe an association of palynomorphs and fossil sharks from the Jagüel Formation at the Ranquil-Có section (36°12'S, 69°30'W; Fig. 1A) in Mendoza. Moreover, we discuss the age and depositional environment of the Jagüel Formation in this part of the basin (Ranquil-Có section) based on sedimentological and palaeontological data. The selachian teeth and dispersed organic matter assemblages provide insights into the composition of the neritic biota leading up to the K–Pg mass extinction in South America.

## Geological setting and previous studies

The Neuquén Basin extends from the active magmatic arc along the Andes in the west, to the Sierra Pintada System and the North Patagonian Massif in the northeast and southeast, respectively. This basin includes sediments that range in age from Late Triassic to Paleogene and hosts one of the most important successions of continental and marine fossil vertebrates and

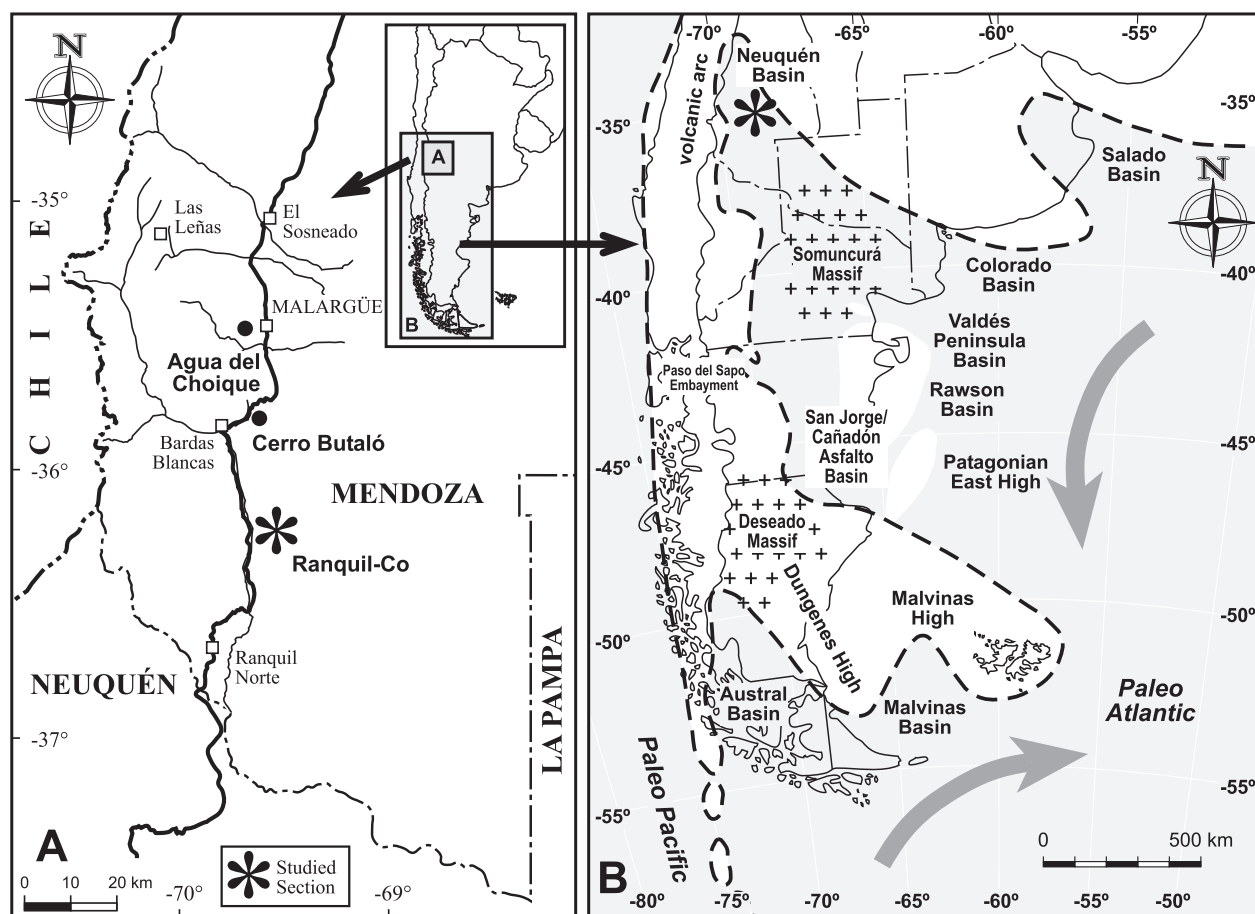


Fig. 1. Location map of the area studied. **A**, Ranquil-Có section, Province of Mendoza, Argentina. **B**, Paleogeographic map of marine basins in southern South America (Patagonia Argentina) showing the Maastrichtian–Early Paleocene Atlantic marine transgression (modified from Náñez & Malumián 2008, Scasso *et al.* 2012).

invertebrates from South America (Macellari 1988). It represents the infill of a retroarc basin that transformed into a foreland basin during the Late Cretaceous (Legarreta & Uliana 1991). The Neuquén Basin sedimentary succession was divided by Groeber (1946) into three large cycles: Jurassic (Pliensbachian–Oxfordian), Andico (Kimmeridgian–Cenomanian) and Riográndico (Cenomanian–Paleocene) cycles related to transgressive–regressive episodes.

The Riográndico cycle comprises two thick units: the Neuquén and Malargüe groups. The Malargüe Group represents deposits of an Atlantic transgression that covered northwestern Patagonia and southern Mendoza province during the late Campanian–Maastrichtian (Fig. 1B) and persisted in the southeastern part of the basin up to the Danian (Náñez & Concheyro 1997, Keller *et al.* 2007, Náñez & Malumián 2008).

Several authors have suggested that a narrow and elongate embayment (*ca* 120 km wide), opening to the Atlantic Ocean, developed in Mendoza during the latest Cretaceous (Uliana & Biddle 1988, Barrio 1990). This paleogeographic interpretation is based on the sedimentological studies of the Malargüe Group, which comprise freshwater to marginal marine facies (Loncoche Formation), marine facies (Jagüel and Roca

formations) and finally fluvial facies (Pircala Formation), representing a complete transgressive–regressive cycle that lasted from the late Campanian? to the Paleocene. From a sequence stratigraphic perspective, the Malargüe Group has been divided by various authors into eight (Legarreta *et al.* 1989) or five major depositional packages (Parras *et al.* 1998).

Sedimentological evidence indicates a progressive marine influence from the base of the Loncoche Formation (tide-dominated delta and littoral sabkhas) to the overlying Jagüel Formation (marine shelf facies; González Riga & Parras 1998, González Riga 1999).

The Jagüel Formation consists of green to greyish-yellow calcareous siltstones and mudstones. The top of this unit is recognized by the occurrence of the first bioclastic limestone beds of the Roca Formation, following the criteria of Bertels (1969), Andreis *et al.* (1974) and Uliana & Dellape (1981), among others. This formation is well exposed from southwestern Mendoza (the northwestern part of the Neuquén Basin) to Neuquén, Rio Negro and La Pampa provinces (the southeastern part of the basin).

The Jagüel Formation (30–50 m thick) in the southern Neuquén Basin (Rio Negro and Neuquén provinces) represents relatively deep marine facies (mid- to outer

shelf environments) with characteristic subtidal microfossils (foraminifers, calcareous nannofossils and palynomorphs, mainly dinoflagellate cysts) and invertebrate macrofossils (molluscan assemblages; Concheyro & Villa 1996, Papú *et al.* 1999). In that part of the basin, the marine environment persisted into the Paleocene. Náñez & Concheyro (1997) distinguished two intervals within the Jagüel Formation based on microfossil studies: a late Maastrichtian interval hosting the nannofossils *Micula murus* and *Nephrolithus frequens* and a Paleogene section, subdivided on its microfossil content into lower and upper Danian intervals. Keller *et al.* (2007) also recognized a Maastrichtian interval but suggested a hiatus at the base of the Paleogene (early Danian) with the planktic foraminiferal zone P1c and the nannofossil NP1b zone immediately above it.

Vertebrate remains are relatively common in the Jagüel Formation. Outcrops in northern Patagonia (Río Negro Province) have yielded several specimens of elasmosaurid plesiosaurs cf. *Mauisaurus* sp. and *Tuarangisaurus? cabazai* (Gasparini *et al.* 2003). Likewise, the ichthyofauna of the Jagüel Formation in Río Negro Province includes six chondrichthyan taxa (*Serratolamna serrata*, *Squalicorax pristodontus*, *Cretalamna appendiculata*, *Carcharias* sp., *Odontaspis* sp. and cf. *Pseudohypolophus mcultyi*) and two Teleostei (aff. *Enchodus ferox* and aff. *E. gladiolus*; Bogan & Agnolin 2010). The specimens assigned to *Pseudohypolophus mcultyi* by the latter authors were later reassigned to *Hypolophodon patagoniensis* (Cione *et al.* 2012). Cranial and postcranial material of a sea turtle (*Euclastes meridionalis* de la Fuente & Casadío) was collected at the Cerro Azul locality (de la Fuente *et al.* 2009) from Danian beds of the Jagüel Formation. The lithology of the Jagüel Formation is homogeneous across nearly the whole basin, comprising massive fossiliferous calcareous, yellowish-green to olive-green mudstones, with minor intercalations of fine-grained sandstones (Barrio 1990, Scasso *et al.* 2005).

In the northwestern part of the Neuquén Basin (Mendoza Province, this paper) the Jagüel Formation is represented only by 10–30 m thick deposits representing late Maastrichtian inner shelf facies. At the Cerro Butaló section, Prámparo & Papú (2006) reported the presence of the biostratigraphically significant dinocyst *Disphaerogena carposphaeropsis* (Wetzel) Sarjeant, 1985, at the base of the formation. This worldwide marker has its first appearance datum (FAD) at 67 Ma (Williams *et al.* 2004). Casadío *et al.* (2005) mentioned the presence of characteristic late Maastrichtian marine molluscs in this area (corresponding to Zone CC26; Perch-Nielsen 1985) incorporating elements from the Weddellian Province and warm-water regions. Gasparini *et al.* (2001) described mosasaurids and plesiosaurs from the base of the Jagüel Formation, 75 km south of Ranquil-Có at the Liu Malal section.

The Ranquil-Có section is located on the western border of the volcanic area of Payunia. In this area,

Upper Cretaceous strata of the Neuquén and Malargüe groups are complete and crop out in an asymmetrical fold, which has a hinge line that dips to the north. At this section, the Jagüel Formation is 25 m thick and yields sparse vertebrate remains and some marine molluscs (Casadío *et al.* 2005). The shark teeth and palynomorphs we describe here occur in a massive green-yellow calcareous mudstone, with minor intercalations of fine-grained calcareous sandstones (González Riga *et al.* 2010; Fig. 2).

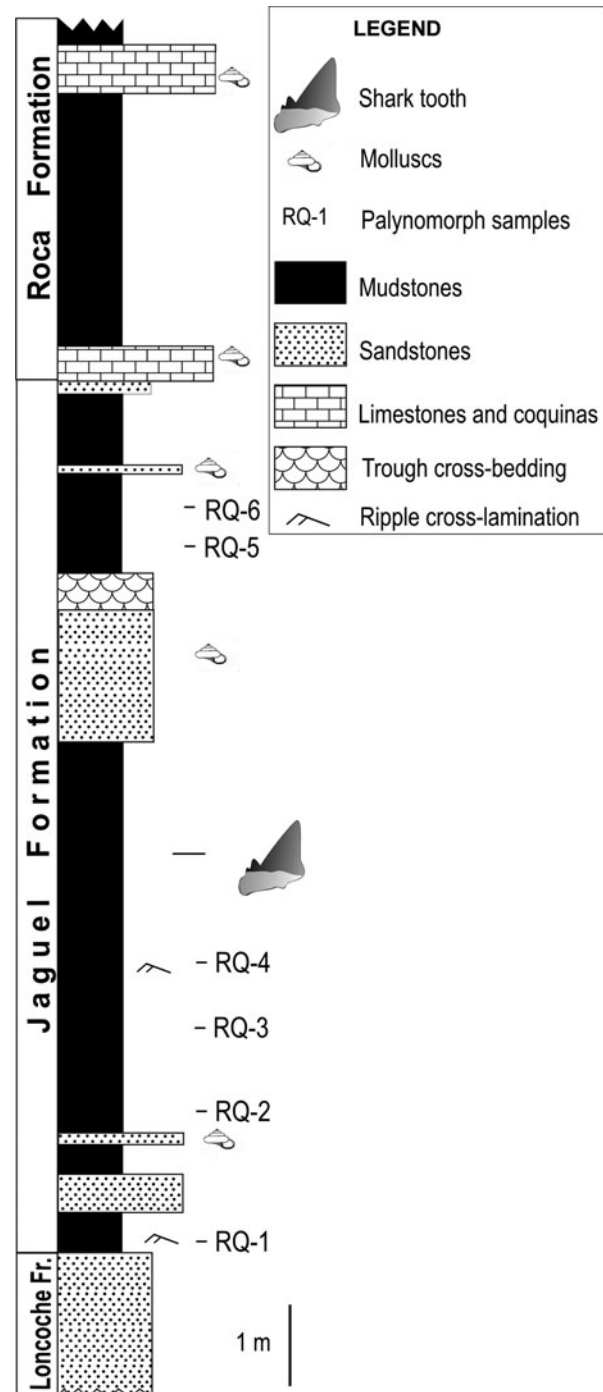


Fig. 2. Stratigraphic column of the Jagüel Formation at the Ranquil-Có section, indicating the sampling levels.

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2012) and it is assignable to *Squalicorax*. It differs from several species of the genus (*S. falcatus*, *S. baharijensis*, *S. coquandi*, *S. africanus*, *S. primaevus* and *S. curvatus*; see Cappetta 1991, Welton & Farish 1993, Siverson 1996, Cappetta & Case 1999, Bardet *et al.* 2000, Vullo 2005, Siverson *et al.* 2007, Vullo *et al.* 2007, Shimada 2008, Bourdon 2011, Cappetta 2012) by the following combination of characteristics: the tooth is large, broad, slim and bent towards the rear; the mesial edge is convex except near the tip; the distal edge is convex; the tip of the cusp does not extend distally beyond the distal demarcation of the root; the distal notch is absent (the transition between the distal cutting edge and distal blade is indistinct); cutting edge serrations are very coarse and irregular near the tip of the cusp; and the labial face is flat.

Shimada & Cicimurri (2005) suggested that, despite all the factors that hinder determination of the exact phylogeny, it is intriguing that if representative teeth of each North American *Scindocorax* and *Squalicorax* species are arranged according to the sequence of their first stratigraphic occurrence, at least six morphological trends are discernible from the earliest-emerging species (*S. volgensis*) to the latest-emerging species (*S. pristodontus*). These trends are: (1) teeth become larger and labiolingually thinner; (2) the cusp becomes more erect; (3) the mesial edge becomes highly convex; (4) the transition between the distal cutting edge and distal blade becomes less distinct; (5) serrations become coarser and more complex; and (6) the root becomes thinner and longer.

The tooth most resembles that of the Maastrichtian species *Squalicorax pristodontus*, especially in its slightly distinct transition between the distal cutting edge and distal blade.

Family indeterminate

***Serratolamna* Landemaine, 1991**

cf. ***Serratolamna serrata*** (Agassiz, 1843) (Fig. 3B, C)

**Material.** IANIGLA-PV-4001, 402: Two incomplete teeth.

**Remarks.** Although fragmentary, two teeth from the Jagüel Formation appear to be assignable to *Serratolamna* (Fig. 3). *Serratolamna* teeth are sometimes misidentified for *Cretalamna appendiculata*. However, they differ in: (1) there are generally at least two pairs of lateral cusplets in the former, whereas only one pair is usually present in the latter; (2) the central cusp in the former tends to show a strong distal curvature compared to that in the latter species; (3) the central cusp of *Serratolamna* teeth is more compressed labiolingually compared to that of *C. appendiculata* teeth; (4) the central cusp of *Serratolamna* teeth tends to be particularly thin near the mesial and distal corners on the lingual face,

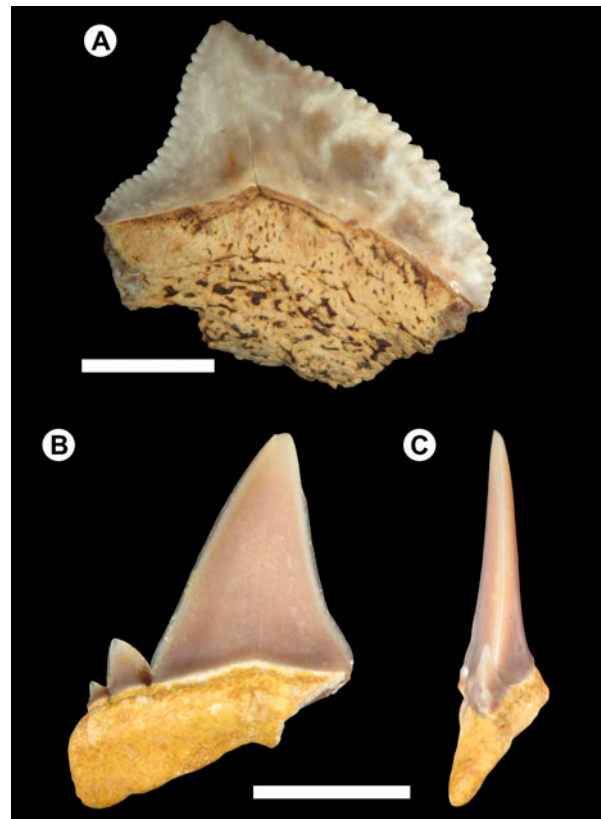


Fig. 3. Shark teeth. A, IANIGLA-PV-400: *Squalicorax pristodontus*. B, C, Lingual and lateral views of IANIGLA-PV-4001: cf. *Serratolamna serrata*. Scale bars = 10 mm.

whereas *C. appendiculata* teeth do not show such a tendency (Shimada & Brereton 2007).

The type species of the genus is *Serratolamna serrata*, a very common taxon, already known from the Jagüel Formation (Bogan & Agnolin 2010). It is unclear whether *Cretalamna maroccana*, *C. caraibaea* and *C. biauriculata* should be included in *Serratolamna* (see comments by Underwood & Mitchell 2000). Another putative *Serratolamna* species (*S. khderii*) differs from *S. serrata* and the material from Mendoza because of its smaller size and the presence of more or less marked lingual folds on most of the teeth (Vullo 2005).

Lamniformes indet.

**Material.** IANIGLA-PV-403 to 414: Eleven fragmentary teeth.

#### *Palynomorphs and organic matter*

RQ2 to RQ6 proved productive for palynomorphs. The palynomorph association recovered is well preserved (mainly the algae) but it is very low in diversity (10 taxa) and abundance (0.6–6.4% of the total association); reliable quantitative analyses were, therefore, not possible at species level.

Prasinophycean algae (*Cymatiosphaera* Wetzel ex Deflandre, 1954, *Pterospermella* Eisenack, 1972 and *Tasmanites* Newton, 1875) dominate the association



(Fig. 4). Sparse dinoflagellate cysts and only a few land-derived sporomorph (trilete spores and bisaccate pollen grains) are also present (Table 1).

The Jagüel Formation *Tasmanites* specimens are hollow, spherical, thick-walled vesicles (diameter

50–90 µm; wall 4–5 µm thick) with some pores that rarely penetrate the entire wall (Fig. 4A, B), and otherwise ornamented with polygonal poroids (depressions) and with bacula distributed irregularly over the entire surface. The *Cymatiosphaera* complex (Fig. 4C–F) is

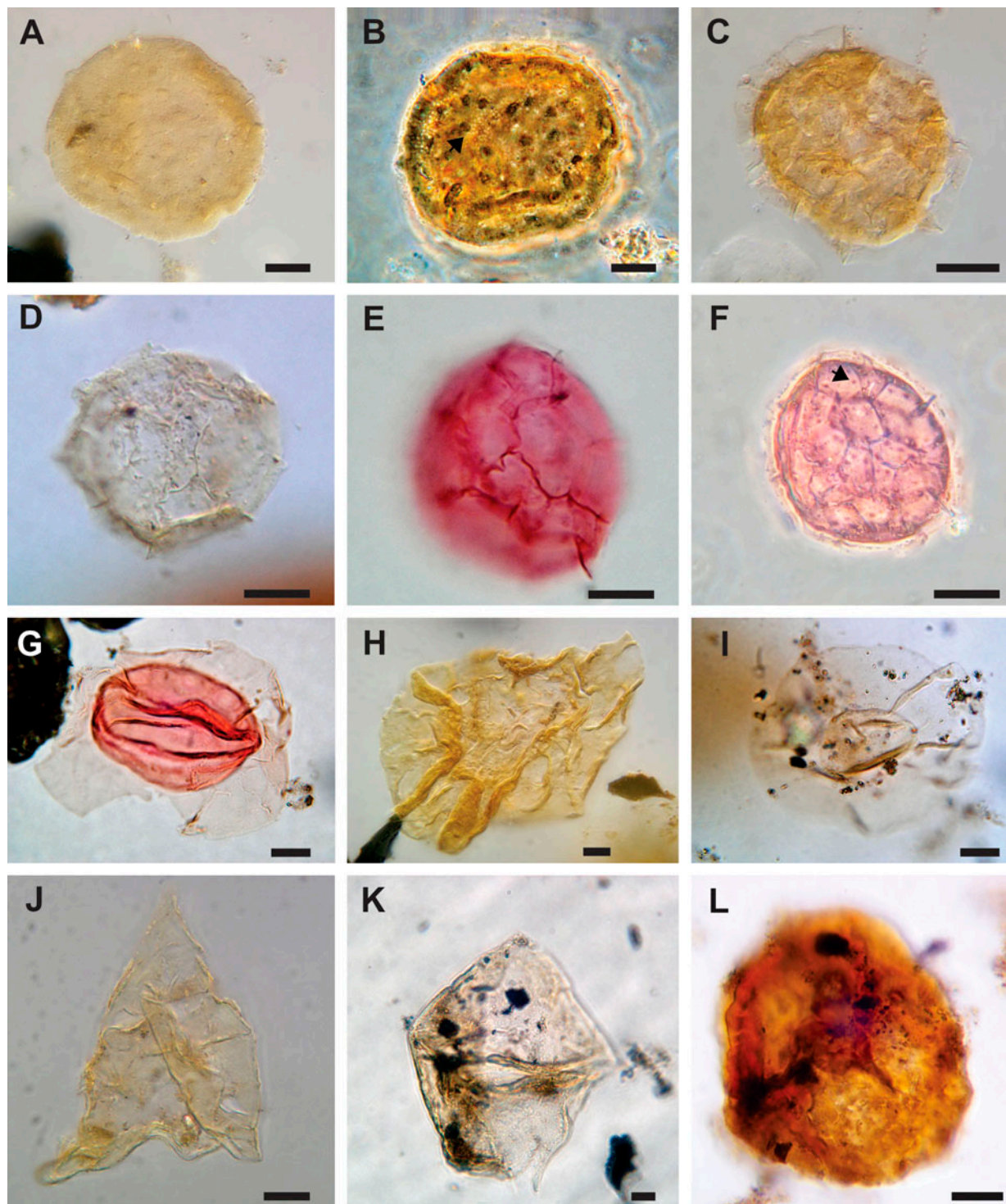


Fig. 4. Palynomorphs. A, B, *Tasmanites* sp. MPLP8679b (RQ3): P27/4 the arrow indicates the polygonal poroids (depressions) and the bacula distributed irregularly over the entire surface. C–F, *Cymatiosphaera* complex. C, MPLP8682a (RQ6): F37/3. D, MPLP8681c (RQ5): O41/4. E, F, MPLP8680b (RQ4): P32/3 specimen showing round granula (indicated by an arrow) distributed alongside the septa. G–I, *Pterospermella* spp. G, MPLP8678b (RQ2): J23/1 specimen with the release suture. H, MPLP8682b (RQ6): J41/1. I, MPLP8679d (RQ3): O43/3. J, K, Undetermined peridinoid cysts. J, MPLP8682a (RQ6): O32/4. K, MPLP8681b (RQ5): T36/4. L, *Leptolepidites* sp. MPLP8678a (RQ2): M31/3. Scale bars = 10 µm.

represented by numerous spherical vesicles (32–60  $\mu\text{m}$ ) with the surface divided into polygonal fields surrounded by 2–5  $\mu\text{m}$  high ridges and ornamented with conspicuous rounded granula distributed alongside the ridges (Fig. 4F). *Pterospermella* encompasses spherical vesicles (total diameter 60–100  $\mu\text{m}$ ) with a broad equatorial flange (20–30  $\mu\text{m}$ ) and radial folds (Fig. 4G, H, I); many of the specimens show the excystment suture (Fig. 4G). Dinoflagellate cysts are very scarce. We recognized a few indeterminate 60–115  $\mu\text{m}$  long transparent peridinioid cysts (Fig. 4J, K) and one broken specimen belonging to the *Palaeocystodinium/Andalusiella* complex. The terrestrial-derived sporomorphs are impoverished. Less than 10 specimens were documented in all the studied material and these represent robust smooth and ornamented trilete spores (Fig. 4L; *Deltoidospora* sp., *Leptolepidites* sp., *Ceratosporites* sp.) and some bisaccate pollen grains.

There is only one previous report of palynomorphs from the Jagüel Formation in Mendoza. The Jagüel Formation yielded an important marine palynological association from the Butaló section (Prámparo & Papú 2006), 40 km northwest of the Ranquil-Có section (Fig. 1), dominated by dinocysts (75–94%) represented mainly by complex *Spiniferites/Achomosphaera* but with prasinophytes such as *Pterospermella australiense* (Deflandre & Cookson) Eisenack, 1972 in very low

numbers in the basal part of the section. The difference in the palynological composition of the Jagüel Formation between the Cerro Butaló and Ranquil-Có localities reflects their different depositional settings within the basin. The high ratio of dinoflagellate cysts to terrestrial palynomorphs and high cyst diversity, associated with foraminifer linings found at the Cerro Butaló section, are indicative of more open marine conditions compared to the Ranquil-Có association (mainly represented by prasinophytes), which probably reflects inner neritic conditions (Prauss 1989, Brocke & Riegel 1996). A significant fraction of the organic matter (OM) recovered from marine samples are of allochthonous origin, derived from terrestrial plants (cuticles, woody fragments, opaque and translucent phytoclasts, pollen and spores). Their sedimentation is controlled by hydrodynamic processes and their abundance generally decreases seawards (Traverse 1994, Batten 1996, Zavattieri *et al.* 2008). Therefore, quantitative or qualitative analyses of OM can give us some information on environmental dynamics. We distinguished three organic matter assemblages (A, B, C: palynofacies) through the investigated profile based on changes in the proportions of the dispersed organic constituents (Table 1).

Assemblage A was represented only in sample RQ1 and is characterized by a high percentage of mainly granular amorphous organic matter (AOM, 94%) and

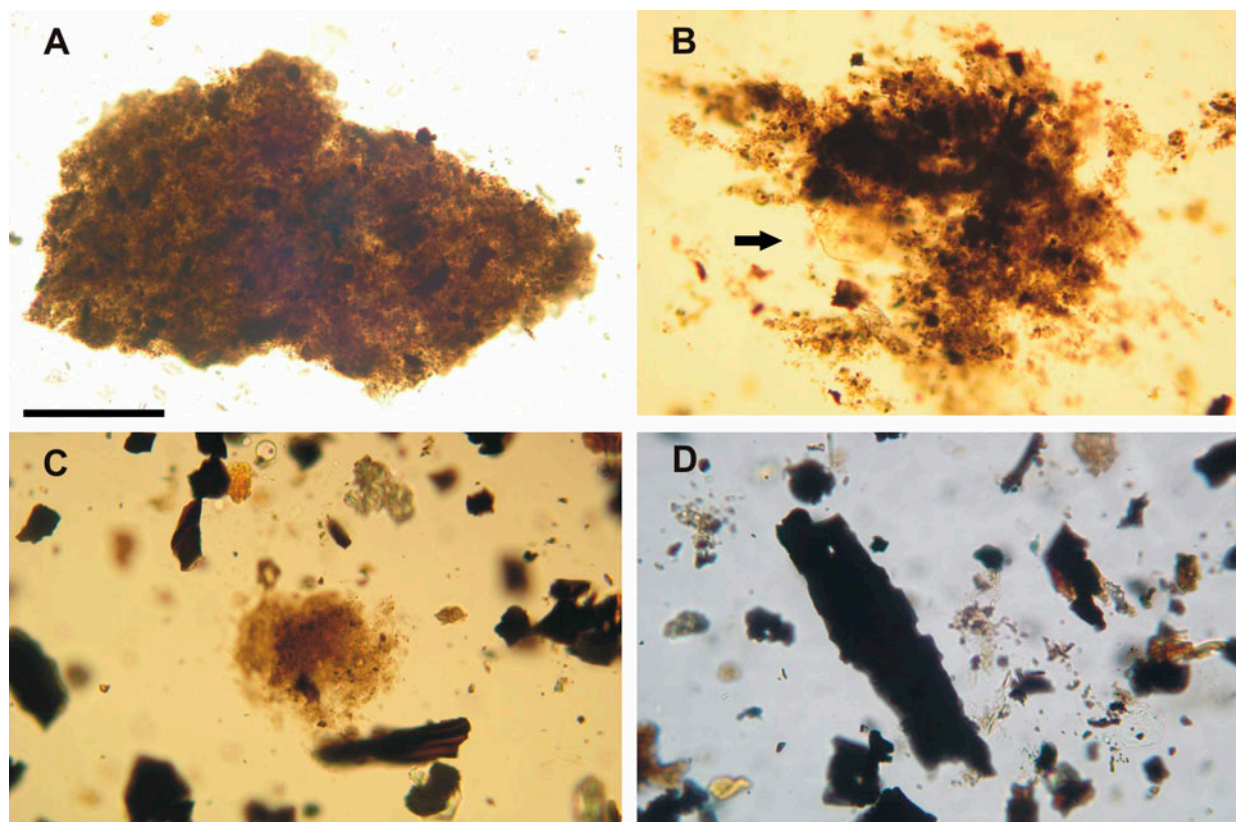


Fig. 5. Photomicrographs of representative samples of the three organic matter assemblages (palynofacies) from the Jagüel Formation, Ranquil-Có section. **A**, RQ1 granular amorphous organic matter (AOM) (Ass. A). **B**, RQ2 *Tasmanites* sp. (indicated with an arrow) and granular AOM (Ass. B). **C**, RQ2 opaque equidimensional phytoclasts, AOM and translucent structured phytoclast without definitive biological structure (Ass. B). **D**, RQ5 opaque lath-shaped phytoclast with corroded edges (210  $\mu\text{m}$ ) (Ass. C).



lacks palynomorphs (Fig. 5A). Assemblage B is represented by three consecutive samples, RQ2 to RQ4, with abundant equidimensional opaque phytoclasts (33–77%). Among the palynomorphs, prasinophytes (4–5.2%) are the most important. Tasmanaceans are the most abundant (3.2%; Fig. 5B, C) in RQ2 and specimens belonging to *Cymatiosphaera* are dominant in RQ3 and RQ4. *Pterospermella* is represented in RQ2, RQ3 and RQ4 by only a few specimens. In RQ4, translucent phytoclasts without definitive biological structure constitute 5.4% of the assemblage. Assemblage C corresponds to samples RQ5 and RQ6, and is characterized by abundant opaque phytoclasts (70.6–94%) but with an evident decrease in the number of prasinophytes (<1%) and with lath-shaped opaque phytoclasts in RQ5 (17%). Many of these phytoclasts exceed 200 µm in diameter (Fig. 5D), with edges corroded by microorganisms.

The AOM is abundant at the base of the section and decreases to the top. Generally, a high AOM concentration indicates low-energy, stagnant, oxygen-depleted environments (van der Zwan 1990, Tyson 1993). The proportion of equidimensional small phytoclasts versus lath-shaped woody fragments is remarkably high in the entire section, but especially from RQ2 to the top. Phytoclasts dominate this interval (RQ2–RQ4). The percentage of phytoclasts is commonly high in oxidizing environments, in which the highly resistant nature of lignin results in woody debris being the only preserved organic material. Woody debris commonly survives prolonged transport within the basin and reworking in shelf settings (Tyson 1993). Generally, the ratio of opaque to translucent phytoclasts increases basinwards due to fractionation processes and the higher preservation potential of opaque particles (Götz *et al.* 2008). Assemblage B palynomorphs occur in massive green-grey mudstones. The massive nature of the mudstones was interpreted by Scasso *et al.* (2005) and Barrio (1990) as representing deposition in a reasonably well-oxygenated environment with intense bioturbation. The few sporomorphs (land-derived pollen and spores) recovered in samples might be due to taphonomic processes (e.g., subaerial oxidizing conditions under a semi-arid climate), which may have degraded the pollen and spore population and selectively concentrated opaque phytoclasts. Based on facies analyses of the Malargüe Group, Barrio (1990) considered that a semi-arid climate favoured deposition of mixed carbonate-siliciclastic lithologies and evaporites in the basin. In the section, samples RQ5 and RQ6 are separated from the samples corresponding to Assemblage B by a fine sandstone bed with trough cross-bedding at the top, probably indicating more nearshore conditions. A sample above sandstone bed RQ5 contains less-sorted organic particles with slightly more lath-shaped phytoclasts (>200 µm in maximum dimensions) and a decrease in marine components compared to samples RQ2–RQ4. This trend of abundant lath-shaped woody fragments

associated with proximal marine settings was also observed in the Upper Cretaceous of the Votocian Basin, southeastern France (Götz *et al.* 2008), and in the Middle Jurassic of the Neuquén Basin, Argentina (Martínez *et al.* 2008).

## Discussion

### *Age of the assemblages*

The lamniforms Anacoracidae and the species *Serratolamna serrata* are only known in the Cretaceous, and both became extinct at the Cretaceous–Paleogene transition (Welton & Farish 1993, Bourdon 2011, Cappetta 2012). *Serratolamna serrata* is particularly common in Maastrichtian beds. Therefore, the record of these taxa in Mendoza is consistent with the Maastrichtian age assigned to the Jagüel Formation in this region, as defined by dinocysts and molluscs (Casadio *et al.* 2005, Prámparo & Papú 2006).

Unfortunately, the palynological association recovered in the Ranquil-Có section consists almost exclusively of prasinophyte algae. This group originated in the Precambrian and lacks biostratigraphic value in Mesozoic–Cenozoic assemblages (Stover *et al.* 1996).

### *Palaeoenvironmental inferences*

The Jagüel Formation was interpreted by Uliana & Dellape (1981) to have been deposited in a marine environment; the lower part of the formation corresponds to inner neritic facies deposited under water depths of 50–100 m.

*Squalicorax pristodontus* and *Serratolamna serrata* have been reported from a few South American localities (e.g., Brazil, Souza Lima *et al.* 2002; Venezuela, Carrillo Briceño *et al.* 2008). Recently, Bogan & Agnolin (2010) described abundant and well-preserved examples of these taxa from the Jagüel Formation in Río Negro Province, northern Patagonia (Cerro Dientes 39°43.8'S, 66°40.2'W). The Ranquil-Có association includes active neoselachian sharks probably living in neritic and nearshore environments (Underwood & Mitchell 2000). Although sharks are opportunistic and range through many marine and estuarine environments, it is fair to infer that these Cretaceous sharks had behaviours analogous to modern active sharks patrolling shallow environments along oceanic margins (Becker *et al.* 2004).

The species of *Squalicorax* and *Serratolamna* were wide-ranging in temperate and warm seas (Cappetta 1991, Welton & Farish 1993, Cappetta & Case 1999, Bardet *et al.* 2000, Vullo 2005, Siverson *et al.* 2007, Vullo *et al.* 2007, Shimada 2008) and unknown at high latitudes (Richter & Ward 1990, Cione 1996). This is consistent with the report by Casadio *et al.* (2005) of warm-water bivalve species, such as *Plicatula georgiana* Fritzsche, 1919 and *Camptonectes tutorae*

Casadío, Griffin & Parras, 2005 in the Jagüel and Roca formations at the Ranquil-Có and Cerro Butaló sections.

Prasinophyceans are unicellular green algae with a two-stage life cycle: a motile flagellate stage (quadri-flagellate) and a non-motile stage (phycoma). As the motile cell and young phycomata are similar in different species, most are identifiable only via the empty phycoma (Tappan 1980). The prasinophyte cyst stage is highly resistant and is recognized in the fossil record since the Palaeozoic. Relatively little is known about the ecology of modern prasinophytes (Tyson 1995). Prasinophycean algae are mainly oceanic; others may occur in tidal pools, brackish water and even freshwater (Tappan 1980), but they are uncommon in terrestrial lacustrine environments (Brocke & Riegel 1996). The taxa present in our study are marine species as their extant equivalents, *Pterosperma* (*Pterospermella*, *Cymatiosphaera*) and *Pachysphaera* (*Tasmanites*), occur in marine phytoplankton communities of different depths (Guy-Ohlson 1996). The phycomata are commonly conspicuous components of both shelf and oceanic sediments deposited under dys-oxic to anoxic conditions (Tyson 1993, 1995). Termed 'disaster species' by Tappan (1980), their ecological tolerance seems to be of a much wider range in comparison to other groups (Götz & Feist-Burkhardt 2012). High percentages of prasinophytes are indicative of stable stratified water masses with low production of cyst-forming dinoflagellates and low levels of reworking of dinocysts from adjacent shelf areas, and/or dys-oxic-anoxic basinal sediments with low sediment accumulation rates (Tyson 1995). The Jagüel Formation in the studied section was deposited in inner neritic conditions. Salinity stratification, therefore, seems to have been the main factor controlling mass occurrences of prasinophytes. They are more common in restricted marine environments in nearshore areas (Prauss 1989, Brocke & Riegel 1996) including restricted (hypersaline?) and partly anoxic, lagoon and shallow-water carbonate facies (Tyson 1993). These conditions favour inhibition of dinocyst production and, therefore, a relative increase in prasinophytes. Mudie *et al.* (2011) recently discussed the importance of non-pollen palynomorphs as indicators of salinity and environmental change in the Caspian–Black Sea–Mediterranean corridor. The data show that *Pterosperma* (*Cymatiosphaera*) dominates only in eutrophic waters with lower salinity and is absent in oligotrophic marine-hypersaline Aegean waters. In contrast, *Pterospermella* has only been reported from the hypersaline Red Sea. In summary, the dominance of prasinophytes of diverse genera and varied salinity preferences in our samples probably denotes stratified inner neritic waters. Such restricted conditions were inappropriate for dinocyst production, which explains the presence of only a few, very transparent, peridinioid cysts in our samples.

#### *Regional significance of the Jagüel Formation association*

The break-up of Western Gondwana generated the first Atlantic marine transgression that reached the foothills of the southern Andes in the Late Cretaceous. The Atlantic marine transgression into the Neuquén Basin defines a regional change in the foreland slope associated with a eustatic sea-level rise (Barrio 1990, Aguirre-Urreta *et al.* 2011). The Cretaceous uplift of the Andes was episodic along the flanks of the Neuquén Basin. The episodic uplift contributed to an eastwards migration of the thrust front and the volcanic arc. These episodes were controlled by the break-up of Western Gondwana and the beginning of absolute motion of South America to the west (Aguirre-Urreta *et al.* 2011). The Malargüe Group (Loncoche, Jagüel and Roca formations) represents the cycle of marine deposition related to the opening of the Atlantic Ocean. The Jagüel Formation represents the maximum marine influence in the area (Legarreta *et al.* 1989).

The records of neoselachian shark teeth between 36° S (Ranquil-Có, Mendoza) and 39° S (Cerro Dientes, Rio Negro) are indicative of the deep penetration of marine conditions into the northern part of the basin. *Squalicorax* and *Serratolamna* are taxa widely distributed in warm temperate and warm Maastrichtian southern seas (Cappetta 2012). The presence of warm-water species in southern middle latitudes is also represented in other fossil groups. Near the K–Pg boundary and during the Danian, the Weddellian molluscs were replaced by warm-water taxa from Brazil, the Caribbean and northern Africa (Casadío *et al.* 2005, Aguirre-Urreta *et al.* 2008). Prámparo & Papú (2006) estimated an age of *ca* 67 Ma or younger for the Jagüel Formation in the northwestern part of the basin based on the FAD of the dinocyst *Dispahaerogena carposphaeropsis* recovered from equivalent strata in the Cerro Butaló section. In the central part of the basin (Neuquén Province), the K–Pg boundary interval is limited to a single thin sandstone bed in the upper half of the Jagüel Formation type section (Scasso *et al.* 2005). However, in the northwestern part of the basin (southern Mendoza), Parras *et al.* (1998) indicated that the K–Pg boundary lies within the continental deposits of the Pircala Formation (which overlies the Roca Formation), but this interpretation is not yet well supported. The Jagüel Formation represents the very latest Maastrichtian in this part of basin, and the K–Pg boundary could be within the Roca Formation limestone. At the Cerro Butaló section (*ca* 50 km northwest of the Ranquil-Có section), the Jagüel Formation yielded an important association of terrestrial and marine palynomorphs with dinoflagellate cysts dominating nearly all samples. Within the Gonyaulacoid cyst group, representatives of the *Spiniferites/Achomosphaera* complex are common species in the Jagüel Formation where they are coincident with high dinocyst/terrestrial palynomorph ratios. However, there are two peaks in

abundance of terrestrial species (>50%) just above the sandstone bed in the middle part of the section (Prámparo & Papú 2006). The same trend of more proximal conditions above the sandstone is also evident in Ranquil-Có, based on the analysis of the dispersed organic matter. In restricted marine environments, palynological correlations between sections are difficult due to disparate associations related to the diverse range of local ecosystems. The less varied marine palynological association recovered from the Ranquil-Có section compared to the Cerro Butaló association could be related to its proximity to the eastern border of the shoreline.

#### *Comparison with other western South American restricted K–Pg marine associations*

An extensive marine incursion took place over large parts of southern South America during the Maastrichtian (Macellari 1988). During the K–Pg transition, the Andean Basin of South America was a subsiding foreland basin, parallel to the Pacific margin (Vajda & McLoughlin 2005). The Bolivian region, situated at the southern end of this elongate basin, experienced episodic marine transgressions that may have originated from northwestern South America (Sempere *et al.* 1997) or from the Atlantic (Marquillas *et al.* 2005) with predominantly continental sedimentation similar to the northern Neuquén Basin. The El Molino Formation and its sub-Andean equivalents (the Eslabón/Flora and Cajones formations) represent the Late Cretaceous in the Republic of Bolivia. Pérez Leyton (1987) studied the palynological content from the Chaunaca and El Molino formations in the Northern Highlands (Altiplano Norte) and Vajda-Santivanez (1999) studied the Rio Flora and Eslabón formations. They recovered a continental association related to a warm and humid environment (with considerable quantities of palm pollen), and without evidence of marine palynomorphs. However, Gayet *et al.* (2001) recovered numerous vertebrate fossils including mixed continental, marine and freshwater taxa from the Pajcha Pata locality (middle Maastrichtian, ca 68.4 Ma: El Molino Formation), which indicate an estuarine or lagoonal depositional environment. However, the authors noted the complete absence of sharks in the fauna. To the south (Salta Group Basin, northwestern Argentina), an extensive and shallow marine transgression emplaced a carbonate succession incorporating oolitic and stromatolitic limestones of the Yacoraite Formation under mainly humid climates until the Danian (Marquillas *et al.* 2005). The Yacoraite Formation hosts fossils of fishes, ostracods, foraminifers, bivalves, gastropods, algae and palynomorphs, all characteristic of restricted marine conditions, which were also confirmed by isotopic evidence (Marquillas *et al.* 2005, 2007). Moroni (1982) studied the palynological content of the Yacoraite Formation and mentioned (without illustrations or descriptions) the presence of a

terrestrial association (*Aquillapollenites magnus* Regali, Uesugui & Santos, 1974, *Crassitricolporites brasiliensis* Herngreen, 1972, *Gabonisporis vigourouxii* Boltenhagen, 1967, among others) with some aplanospores and deflandroid cysts indicating brackish conditions.

Scasso *et al.* (2012) studied marginal marine coarse-grained sediments of the Lefipán Formation (Chubut Province, Patagonia, Argentina) deposited in a tide-dominated delta in an embayment of the tectonically active westernmost end of the Cañadón Asfalto Basin. They noted the presence of shark teeth in coquinas and intraformational conglomerates, but did not provide any taxonomic assignation. The Lefipán Formation consists of Maastrichtian–early Paleogene marine to marginal marine fossiliferous sandstones and mudstones with some intercalated coquinas and conglomerates. Palynological investigations of the Lefipán Formation were carried out by Baldoni (1992) and Barreda *et al.* (2012); both studies mainly described the terrestrial Maastrichtian assemblages derived from a fern and angiosperm-dominated community with common podocarp conifers, diverse Proteaceae, aquatic ferns and abundant palms, suggesting vegetation adapted to warm and humid conditions. Marine associations were only mentioned by way of the presence of the late Maastrichtian marker *Cyclapophysis monmouthensis* Benson, 1976 (*Disphaerogena carposphaeropsis*) and *Damassadinium californicum* (Drugg) Fensome *et al.*, 1993, which indicate a Danian age. There are no references to any other prasinophyte-dominated palynological associations in late Maastrichtian restricted marine environments in this part of South America.

## Conclusions

The fossil assemblage of shark teeth, palynomorphs and dispersed organic matter in the Jagüel Formation of northwestern Neuquén Basin provide additional evidence of the presence of warm-water species in the epeiric seas of middle latitudes towards the end of the Cretaceous, probably related to a climatic warming event. In the Ranquil-Có section, southern Mendoza, teeth from active marine neoselachian sharks highlight a neritic environment. The palynomorph association, composed mainly of diverse and well-preserved prasinophyte algae (*Tasmanites*, *Cymatiosphaera* and *Pterospermella*), favours restricted marine settings. The dispersed organic matter in these strata are concordant with an inner neritic environment (opaque equidimensional phytoclasts and prasinophytes) with evidence of slightly more proximal conditions towards the upper part of the section (a great variety of particle sizes with a slight increase in number of lath-shaped phytoclasts and a decrease in the marine components), and more restricted conditions compared to the Cerro Butaló section. The marine biotas (shark teeth and prasinophytes) confirm the presence of an epeiric sea over northern Patagonia, extending westwards to the volcanic arc on

the western flank of the Andean Cordillera in Mendoza during the latest Cretaceous.

## Acknowledgements

The authors are indebted to Dr S. McLoughlin, V. Bowman and an anonymous reviewer, whose comments and critical observations considerably improved this contribution. Our work was partially supported by CONICET (PIP 713/09 to B. González Riga and M.B. Prámparo), Universidad Nacional de Cuyo (06/M044 to B. González Riga) and Agencia Nacional de Promoción Científica y Tecnológica (PICT 2006-913 to A.L. Cione). We are also grateful to the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (Mendoza) for their laboratory (M.A. Moschetti) and field support and to Rafael Bottero for his collaboration in the composition of Figure 1. The authors are grateful to Erik Marsh (USA) for reviewing the English version of the text.

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