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The Ticó Flora (Patagonia) and the Aptian Extinction Event*

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ABSTRACT. The Aptian Ticó Flora from southern Patagonia has been studied with detail for over 30 years. Fossils are found in the three formations that constitute the Baqueró Group: Punta del Barco the upper, Bajo Tigre the middle and Anfiteatro de Ticó de lower. Two biozones are recognized, viz. the lower *Ptilophyllum* and the upper *Gleichenites* Zone. The *Ptilophyllum* Zone is characterized by the dominance of bennettites-conifers and presence of cycads, ginkgophytes, pteridosperms and pteridophytes. Angiosperms although present in this zone are scarce, represented by both macroscopic remains and palynomorphs. A unfossiliferous stratigraphic interval separates the lower zone from the upper *Gleichenites* Zone. Here ferns are dominant; conifers and cycads are present while bennettites and ginkgophytes are absent. The strong volcanic activity that occurred during the deposition of the Baqueró Group is a probable cause for the drastic floristic change. A brief analysis of the vegetation known in most palaeofloristic regions during the mid-Cretaceous confirms that similar variations occurred at different latitudes and continents. During the Aptian, global vegetational changes, including extinctions at an order level, were initiated and later followed by gradual angiosperm radiation. From a palaeobotanical perspective, the Aptian Extinction Event is an episode of importance, deserving a higher status among other minor events. It may have a similar level that is adscribed to changes at the K-T boundary.

KEY WORDS: Ticó flora, Aptian, Cretaceous, Patagonia, Argentina

INTRODUCTION

The advent and further diversification of angiosperms during the Cretaceous is probably one of the most intriguing and widely discussed subjects in palaeobotany. Studies on the K-T transition and extinction of dinosaurs have added a substantial amount of information directly related to eventual changes of vegetation, in which angiosperms have certainly played an important role. This particular interest has, no doubt, hampered the advance of researches in other, not less interesting fields related to fossil plants. Subjects as why and when did plant groups other than angiosperms declined or disappeared during the late Mesozoic have been remarkably neglected.

During the last decade, studies on extinctions have been steadily developing (Sepkoski 1982, Hart 1996, Freeman & Herron 1997, Hallam & Wignall 1997). They mostly concern marine organisms that are successfully used for fine stratigraphy, which usually is not the case with fossil plants. On the other hand, information on fossil floras of mid-late Cretaceous age is not as abundant as that for marine organisms. The scattered and often poorly studied taphofloras of this period, especially between the Aptian and Cenomanian, yielded information that has not been evaluated in depth, perhaps with the exception of angiosperms and few gymnosperm groups (Hughes 1994, Crane et al. 1995, Krassilov 1997).

The K-T boundary separates two geologic eras. Attention was carefully given to all physical and biological events that occurred around this time: big bio-events are, for instance, dinosaur and ammonite extinctions. But what about vegetation? If putative cosmic

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events, as an asteroid collision are accepted, it is reasonable to suspect that the body impact should have also influenced the total plant world. Yet, this case has not been fully explored up to now. The Cheirolepidiaceae, a conifer family that became extinct around the K-T boundary is an exception. Certainly, there are taxa of lower than family rank, either gymnosperms or ferns, that do not cross that limit. However, this is also true for other Mesozoic boundaries considered to be of a lower rank, in which vegetational changes are not taken to be as important as those that happened at the K-T transition (for instance, the Triassic-Jurassic transition).

EARLY CRETACEOUS PHYTOGEOGRAPHY

Pre-Tertiary gymnosperms have been known for several years: bennettites, caytoniales, corystosperms and pentoxyls, among others, are exclusively mesozoic. Attention was also given to other gymnosperms that are living today as cycads and ginkgos. Although all these groups declined or disappeared during the last part of the Mesozoic, this line of research was never followed as intensively as the coeval angiosperm diversification.

Vakhrameev (1988) recognized four main palaeophytogeographic regions during the Early Cretaceous: Siberian-Canadian, Euro-Sinian, Equatorial and Austral (or Notland). The Siberian-Canadian Region includes three provinces: Lena, Amur and Canada, where the greater variety among cycadophytes occurred during the earliest Cretaceous (Neocomian). The bennettites diminish gradually in the Aptian and persist with a few relics in the basal Albian (Bell 1956, Samylina 1988, Vakhrameev 1988). Mesozoic pteridosperms are apparently unknown in this region, while ginkgophytes, cycads and cheirolepidiaceous conifers are strongly reduced in variety and number, especially after the volcanic events that follow the early Albian time (Samylina 1988).

The Euro-Sinian Region is represented by the European, Potomac, Eastern and Western Mid-Asia and East Asia provinces. Bennettites are known in the Albian of the European Province, while ginkgophytes seem to be absent. In the Potomac Province, bennettites and caytoniales are known in the Aptian to Lower Albian strata but seem to be absent in the mid-late Albian. Ginkgophytes are rarely found in the Aptian. In Mid-Asia little is known about megafloras, although palynological studies show a strong vegetational change in the Aptian (Vakhrameev 1988). Gleicheniaceous spores are very abundant and varied during the Aptian while the few Albian megafloras lack bennettitales and ginkgoales. Aptian megafloras are well known in the Far-East asiatic regions (Krassilov 1967, 1982, Kimura 1980). There, bennettites and ginkgophytes are abundant although with reduced variety and number during the Albian (Vakhrameev 1988). The Equatorial Region has Aptian bennettites in South America (Pons 1982) and Malaysia (Vakhrameev 1988), but ginkgophytes are absent. Albian floras are unknown although there are good palynological records.

The southern or Gondwana Region has a rich Early Cretaceous floristic history. In Eastern Gondwana a strong Aptian volcanism has been dated at 116–118 Ma, in the Intertrappean beds, in the Rajmahal Basin of India (Tiwari & Tripathi 1995). A rich flora is found in this unit, that palynologically resembles other aptian assemblages of a typical mesozoic look. Hill et al. (1999) mention a major vegetational change near the Aptian/Albian boundary, and the disappearance of several plant groups in Australia. They suggest that the mid-Cretaceous interval witnessed the extinction or marked decline of a number of previously prominent gymnosperm and cryptogam groups, notably bennettites, pentoxyls, ginkgophytes, cheirolepidiacean conifers, and genera that may be referred to mesozoic pteridosperms, as *Pachypteris* and *Thinnfeldia* among others.

Precise datings of most of these floras are needed. However, it is evident that their taxonomic composition varies in different geographic regions during the Early Cretaceous. On the other hand, several provinces show a floristic change around the Aptian/Albian transition. In some areas, as in NE Siberia, this change has been related to volcanism.

MIDDLE CRETACEOUS VEGETATION IN PATAGONIA

In Patagonia there are several localities in which mid-Cretaceous plants have been reported (Archangelsky 1967, Baldoni & Ramos 1981, Ruiz 1984, etc.). The best explored area is in Santa Cruz province where the Ticó Flora is located. This flora has been studied by several authors, especially during the last decades (Archangelsky 1963, Menéndez 1966, Herbst 1966, etc.). The age was uncertain until palynological information suggested it was probably Barremian (Archangelsky & Gamerro 1967) or Barremian to Aptian (Romero & Archangelsky 1986), due to the presence of angiosperm leaves. On the other hand, a detailed stratigraphic study of the area where the Ticó Flora is found has revealed the presence of three plant bearing units, referred to Anfiteatro de Ticó Formation the lower, Bajo Tigre Formation the middle and Punta del Barco Formation the upper (Cladera et al. 1999). These three formations are now united into the Baqueró Group. Previously (Archangelsky 1967), these strata were referred to the Baqueró Formation (= Baqueró Group), subdivided into a Lower Member (= Anfiteatro de Ticó Formation) and Upper Member (= Bajo Tigre and Punta del Barco Formations) (Fig. 1). Recently, two isotopic datings were obtained ($^{40}Ar/^{39}Ar$) that confirm the Aptian age of the Baqueró Group: 118.56 ± 1.40 Ma and 119.7 ±0.4 Ma (Corbella, pers. comm.).

The richest assemblages of plant fossils from the Baqueró Group are found in the basal and uppermost units, i.e. Anfiteatro de Ticó and Punta del Barco Formations, respectively (Cladera et al. 1999). Two distinctive biozones were defined in the new stratigraphic scheme: the lower *Ptilophyllum* Zone and the upper *Gleichenites* Zone (Archangelsky 1999, 2001). The distribution of the principal taxa is shown in Table 1 (for a more detailed information, see also Tab. 1 of Archangelsky 2001).

Table 1 is a record of the main genera (including the number of species in each genus) found at different sites in the three formations that integrate the Baqueró Group. A brief analysis of the presence-absence of components demonstrates a total disappearance of bennet-

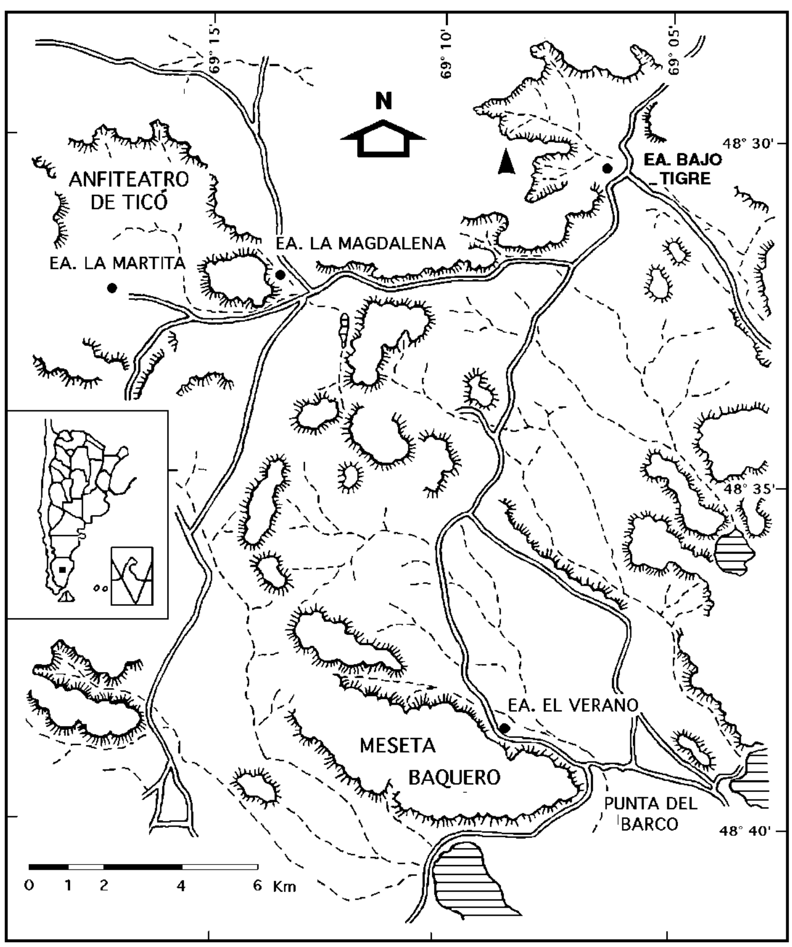

Fig. 1. Map showing the main plant localities

Table 1. Distribution of main genera of fossil plants in the three formations of Baqueró Group and in the two biozones recognized. Numbers in brackets indicate number of species of the genus found in the respective formation(s). The isotipic age at the right bottom corner is placed at the exact stratigraphic position of analysed tuffs

Taxa — Zones / Fms	*Ptilophyllum*	*Gleichenites*	
	Anfiteatro de Ticó	Bajo Tigre	Punta del Barco
Baqueroites	■		
Cladophlebis (3 sp.)	■		
C. psilotoides	■		
Ktalenia	■		
Ruflorinia pilifera	■		
Almargemia	■		
Mesodescolea (2 sp.)	■		
Pseudoctenis (3 sp.)	■		
Sueria (2 sp.)	■		
Ticoa (3 sp.)	■		
Androstrobus (3 sp.)	■		
Cycadolepis (5 sp.)	■		
Dictyozamites (4 sp.)	■		
Otozamites (3 sp.)	■		
Pterophyllum	■		
Ptilophyllum (2 sp.)	■		
Williamsonia (3 sp.)	■		
Zamites (2 sp.)	■		
Allicospermum	■		
Ginkgoites (2 sp.)	■		
Karkenia	■		
Apterocladus	■		
Athrotaxis	■		
Brachyphyllum (5 sp.)	■		
Morenoa	■		
Notopehuen	■		
Squamastrobus	■		
Tarphyderma	■		
Trisacocladus	■		
Hausmannia papilio	■	■	■
Brachyphyllum sp.	■	■	■
Gleichenites vegagrandis	■	▬	■
Ruffordia	■	▬	■
Pachypteris (2 sp.)	■	▬	■
Ruflorinia sierra	■	▬	■
Taeniopteris	■	▬	■
Mesodescolea (2 sp.)	■	▬	■
Araucaria	■	▬	■
Araucarites (2 sp.)	■	▬	■
Podocarpus (2 sp.)	■	▬	■
Tomaxellia (2 sp.)	■	▬	■
Mesodescolea obtusa		■	
Gleichenites sanmartinii		■	■
Nilssonia			■
Pseudoctenis ornata			■
Cladophlebis (3 sp.)			■
Gleichenites (2 sp.)			■
Hausmannia patagonica			■
Sphenopteris (2 sp.)			■

119 Ma

tites in the *Gleichenites* biozone while in the *Ptilophyllum* biozone they were represented by many species belonging to several genera of leaves (*Otozamites, Dictyozamites, Ptilophyllum, Pterophyllum, Zamites*), bracts (*Cycadolepis*) and inflorescences (*Williamsonia*). Pteridosperms, though not very abundant were nevertheless varied, and most became extinct during the crisis, as shown by megafossil remains (leaves of *Pachypteris* and the fructification *Ktalenia*). Similarly all ginkgoalean remains disappeared (leaves of *Ginkgoites, Allicospermum* seeds and the fructification *Karkenia*). Cycads show also a dramatic decline: twenty megafossil taxa are reduced to only two, one species of *Pseudoctenis* and another of *Mesosingeria*. Four cycadean genera (that include 10 species) became extinct: *Ticoa, Almargemia, Androstrobus* and *Sueria*.

Twenty one conifer species are known in the Ticó Flora. Most are absent in the upper biozone. Some genera known with their fructifications have not been found in Punta del Barco Formation: *Notopehuen, Trisacocladus, Squamastrobus, Tarphyderma, Apterocladus*. This may be partly due to preservation (because mummifactions are principally found in the lower sector of the column). However, there is a clear decline in abundance, also confirmed by palynological data: for instance, *Classopollis*, a dominant pollen type in the lower biozone is absent in the upper part of the sequence. In this case it does not mean that members of the Cheirolepidiaceae family became totally extinct, because in younger cretaceous strata this type of pollen is found again, suggesting it was merely a temporary retreat to more suitable habitats in more restricted areas.

Ferns and fernlike fronds, on the contrary, are found all through the column, changing in relative abundance. Gleicheniaceae (*Gleichenites, Gleicheniidites* spores) and Dipteridaceae (*Hausmannia*) are very common in the upper strata. *Cladophlebis, Sphenopteris* and other fronds are found in both biozones. This distribution suggests that ferns have better adapted to environmental stress and changes than many gymnosperms, confirming their ecological plasticity. Palynology adds further information on first records of taxa during the Aptian, notably the fern family Lophosoriaceae with the spore *Cyatheacidites* (Dettmann 1986, Kurmann & Taylor 1987). The diversification of other fern families such as Schizaeaceae, that had a global climax during the Aptian-Albian, is certified by several spore types: *Cicatricosisporites, Appendicisporites, Trilobosporites* or *Klukisporites* (Archangelsky & Gamerro 1967).

Few scattered angiosperm leaf remains are found in the *Ptilophyllum* biozone, but none in the upper. Again, this may be a matter of preservation, rather than extinction. Palynology reveals the presence of the angiosperm pollen *Clavatipollenites* at the base of the column while both, *Clavatipollenites* and *Asteropollis*, another angiosperm grain, are found at the top of the column, in *Gleichenites* zone (Llorens 2000). The group was poorly diversified at its beginnings, although it survived the Aptian event. It may be suspected that the crisis was a beneficial factor for the development of angiosperms, taking into consideration that several gymnosperms declined and retreated, thus leaving new ecological niches that were conquered by this newly developed group of highly evolved plants.

VOLCANISM, CLIMATE AND VEGETATION

It was suggested that during the Aptian a mantle plume in the Pacific produced new oceanic crust increasing the sea level and changing palaeoceanographic conditions by restricting marginal seas (Mutterlose 1998). The drop in humidity and establishment of a dry climate during the Barremian in Europe was related to restrictions of such marginal seas (Raffell & Batten 1990). Therefore, volcanic activity was responsible for a change in climate and also for an Oceanic Anoxic Event (OAE; Bralower et al. 1994).

In Southern Patagonia, a relevant episode related to the development of vegetation during the Aptian (Baqueroan) time is the pyroclastic nature of the sediments. These rocks were deposited during recurrent ash fall, and they covered different environments incorporating the surrounding vegetation (Cladera et al. 1999). The influence of volcanic activity in the Baqueró Group has been previously underscored during detailed anatomical investigations of leaf cuticles (Archangelsky & Taylor 1986, Archangelsky et al. 1995). Accordingly, regional geological data show the existence of a strong arc volcanism, related to the opening of the Atlantic Ocean, dated at 120 Ma and located near the Baqueró area (Ramos 1999).

Changes in stratigraphic distribution of plants in Ticó Flora as shown in Table 1 are certainly related to dramatic environmental vartiations due to severe and recurrent ash fall during a period that was long enough to produce significant differences. A “recovery period” (Hart 1996) between both plant assemblages is probably represented by the mostly sterile beds of the Bajo Tigre Formation. During this time the area was repopulated with new taxa, though survivors and opportunistic species (perhaps also disaster species), such as *Gleichenites* spp., persisted (Kaufmann & Harries 1996). During the recovery interval new communities, exemplified by different components, were finally installed. At a regional scale, the typical plant assemblage that characterizes the *Ptilophyllum* biozone never formed again. Abundance of bennettites and conifers, presence of pteridosperms, diversified cycads and frequent ginkgos, so common in mid-late Jurassic to early Cretaceous times, were replaced by other communities. In Patagonia, during the Albian and Cenomanian plant assemblages mostly lack several of these “older” components. They also have a meager representation of other groups, such as cycads or specific conifers (Romero & Arguijo 1981, Riccardi 1988).

The Patagonian volcanic event is also recorded in Antarctica (Antarctic Peninsula) that has a similar geological history (Hathway & Lomas 1998). There, during the mid-Aptian a flora that is similar in many aspects to that found in the *Ptilophyllum* biozone of the Ticó area, has been studied (Hernández & Azcárate 1971, Césari et al. 1999). No further plant records suggesting a younger cretaceous age close to the Aptian are known for the moment.

SIGNIFICANCE OF THE APTIAN EXTINCTION EVENT (AEE)

The floristic change that defines the two biozones of the Ticó Flora (located in the Patagonia Province, *sensu* Vakhrameev 1988), is another record that reinforces the hypothesis of an AEE. Notably, this event is now registered in the Southern Hemisphere, but this time in a continental environment. It is now possible to confirm that this was a global event, and much more significant than previously thought. The floristic change it generated has been recorded in several localities (provinces) of an ample, almost planetary geographic distribution. The biological variation it produced in the plant kingdom includes decline or disappearance of several gymnosperms and first records of angiosperms. The influence AEE had on both marine and continental biota reinforces the importance of this episode.

It is becoming more and more evident that the Aptian is an important landmark in the evolution of the plant world, and should deserve a higher rank in event biostratigraphy. Certainly, the Mesozoic Era witnessed the dominance and high diversification of gymnosperms (and to some extent of ferns). This situation changed dramatically during the mid Cretaceous, and not so much at the K-T boundary. During the Late Cretaceous a new vegetational model was developed in which angiosperms diversified and later dominated, gymnosperms became more restricted (some even disappeared) and ferns retained their ability to adapt to different ecological situations. At the K-T boundary, this model had already a long history.

If fossil plant records are evaluated in the way Boulter did (Boulter 1996, fig. 1), the Aptian-early Albian interval shows the beginning of angiosperm rise, a strong reduction of the conifer and pteridophyte dominance curve and a faint reduction of “other seed plants” curve. This sketchy interpretation confirms Vakhrameev’s views, on a much broader scale however, in regard to a global mid Cretaceous floristic variation.

This new approach may have further implications, especially in studies of Late Cretaceous continental biota. The angiosperm rise and diversification parallels the evolution of insect world (Labandeira et al. 1994). But on the other hand it is not clear what possible effect this may have had on dinosaur extinction. Was there a change in the trophic chain that led to gigantism and food selection, that was responsible for fitness weakening and adequate response to adverse conditions at that time? Did angiosperms prefer to develop new syndromes for dispersal and reproduction, turning them to be unsuitable for the ingesta that these animals were adapted to in the past?

The level of knowledge achieved with most components of the Ticó Flora, and its precise stratigraphic situation, opens a new and exciting field of research that needs to be completed with information we possess on other organisms, either continental or marine, that integrated the Patagonian biota during the mid-Cretaceous.

CONCLUSIONS

The Ticó Flora is a partial testimony of the Cretaceous history of continental Patagonia. It shows that a strong geologic disturbance was responsible for the extinction of many plant taxa before a repopulation process occurred. During the Aptian a strong volcanic event caused a remarkable vegetational change. Two biozones, the lower *Ptilophyllum* Zone and the upper *Ginkgoites* Zone are characterized by the presence of exclusive taxa. The lower zone consists of an assemblage of typical mesozoic plants, belonging mainly to bennettites, conifers and cycads together with varied ferns. A brief interval of unfossiliferous strata follows until a new type of assemblage, dominated by ferns, especially *Ginkgoites* and *Hausmannia*, is found in a pyroclastic environment, in which bennettites, ginkgophytes and most pteridosperms disappear. Conifers, few cycads and different kinds of ferns integrate this new assemblage.

Patagonian Aptian volcanism took part of a much more extended episode that caused the extinction of many organisms at a global scale. The AEE has been recorded mostly for marine biota. However, the Ticó Flora provides evidence of a major shift in composition of plant communities of the Southern Hemisphere during the mid-Cretaceous. The extent of the Aptian volcanism to neighbouring areas (Antarctica), demonstrates that this intrusive impact played an important role by arranging the areal distribution of plant taxa and influencing their evolution in Western Gondwana.

Finally, the radiation of angiosperms in Southern Patagonia seems to have begun after this volcanic episode. The present evidences suggests that the mid-Cretaceous was a crucial time in the evolution of plant world, and from a palaeobotanical point of view it parallels events that characterize the K-T boundary.

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