

UNIVERSIDADE DO VALE DO RIO DOS SINOS - UNISINOS

Programa de Pós-Graduação em Geologia

Defesa de tese

**PTERIDÓFITAS DO FINAL DO CRETÁCEO DA ILHA LIVINGSTON
(PENÍNSULA ANTÁRTICA) E CERRO GUIDO (PATAGÔNIA CHILENA) E
SUAS IMPLICAÇÕES EVOLUTIVAS, PALEOAMBIENTAIS,
PALEOGEOGRÁFICAS**

Cristine Trevisan



São Leopoldo, agosto de 2018.

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1. Introdução

O conhecimento das plantas fósseis que viveram na Península Antártica e Patagônia até a chegada dos climas mais frios do final do Eoceno (Reguero et al., 2013), permite avaliar a biodiversidade das florestas pretéritas das altas latitudes, auxiliar na compreensão de sua distribuição moderna e sobre os processos adotados em sua dispersão, como resposta às mudanças do clima e da paleogeografia. Nestas paleofloras, as pteridófitas são um elemento importante e demonstraram uma fácil adaptação aos diversos tipos de solos e às condições instáveis criadas pelos processos tectônicos próximos.

Bem estabelecidas desde o final do Carbonífero, as pteridófitas refletem o sucesso evolutivo de um grupo cujo registro evidencia três episódios de grande irradiação (Rothwell e Stockey, 2008). O primeiro é marcado, ainda no Paleozóico, pelo aparecimento das famílias basais de leptosporangiadas (p. ex., Osmundaceae, Gleicheniaceae) e de formas gigantes, como *Psaronius* (Rothwell, 1991). A segunda irradiação data do início do Mesozoico, quando passam a dominar os mais diversos ambientes. Neste período, e afetadas pela extinção do Triássico-Jurássico e a aridez que irá caracterizar as áreas do interior da Laurásia e Gondwana, muitos grupos (p. ex. Cyatheaceae) dispersaram, adaptando-se às temperaturas mais amenas das altas latitudes, em especial, naquelas sob influência oceânica (Collinson, 2001; Skog, 2001). A última irradiação coincide com o final do Cretáceo e responde aos eventos de separação dos continentes, soerguimento inicial dos Andes, e ao súbito enriquecimento de CO₂ na atmosfera (meteorito ou vulcanismo?), que afetaram o clima e as conexões terrestres, criando barreiras marítimas que incentivaram o endemismo e novas áreas costeiras marinhas. Inúmeras novas bacias se formaram, muitas invadidas pelos novos oceanos e que atestam intervalos de queda nas temperaturas, no final limite Campaniano-Maastrichtiano e no do Maastrichtiano nas altas latitudes. As ligações terrestres, em parte mantidas entre a América e a Antártica, e por mais tempo que em outras áreas do Gondwana, serão cruciais para a vida nos ambientes subaéreos e para a compreensão dos modernos biomas do Hemisfério Sul e das novas florestas que irão cobrir as áreas temperadas do globo (Leppe et al. 2012). Novos grupos de pteridófitas surgem neste momento (p. ex., Aspleniaceae, Dryopteridaceae, Pteridaceae e

Polypodiaceae), e pela primeira vez desde o Paleozóico, garantem sua presença na moderna vegetação (Rothwell e Stockey, 2008).

O objetivo deste estudo é complementar o cenário a partir daí estabelecido, com foco nas altas latitudes do Sul. Para tanto, dois estudos de caso, realizados em associações fossilíferas depositadas em níveis do final do Cretáceo, buscam as possíveis ferramentas a partir do estudo das paleofloras, que ampliem a compreensão sobre os processos que modificaram a geografia do globo e conformaram a vida que conhecemos.

O primeiro artigo trata de fósseis relacionados ao gênero *Thyrsopteris*, forma endêmica e relictual, hoje exclusiva das florestas das ilhas do Arquipélago de Juan Fernández (Greimler, 2013). Identificados pela primeira vez para a localidade de Hanna Point na Ilha Livingston (Península Antártica), inserem-se nos objetivos almejados e haviam sido preliminarmente informados por Leppe et al. (2007).

No segundo artigo é analisada uma ocorrência inédita de fósseis de pteridófitas em níveis do Campaniano da Formação Tres Pasos, expostos no Cerro Guido, Patagônia chilena (Yabe et al., 2006). Além de sua riqueza em fósseis marinhos e continentais, a sucessão de Cerro Guido atesta a gradativa queda do nível global do mar no final do Cretáceo e os primeiros efeitos do tectonismo andino, que resultaram na formação da bacia de retroarco (Bacia de Magalhães). Todos estes aspectos tornaram os depósitos de Cerro Guido mundialmente famosos e reconhecidos em sua importância desde o final do século XIX (Kurtz, 1902; Menendez, 1966, 1972; Hunnicken, 1971). A presença de restos de plantas em alguns de seus níveis é uma ferramenta importante para a distinção dos contextos de mar profundo para aqueles transicionais costeiros da Formação Dorotea.

Nas análises foi levada em conta a vocação da área de aplicação em Paleontologia Aplicada, do PPGeo, na busca dos tipos de contextos geológicos aos quais se associam as assembleias fósseis, na busca de ambientes modernos comparáveis e que possam servir como análogos às reconstituições paleoambientais. Dentre os objetivos destaca-se ainda a observação da afinidade de grande parte dos grupos modernos de pteridófitas, e em especial dos fetos arborescentes (Cyatheaceae), aos ambientes insulares de regiões sujeitas a vulcanismo de arco.

1.1 Hipóteses

Neste contexto, e unindo os dados prévios disponíveis (e.g. Cantrill and Poole, 2012; Reguero et al., 2013) àqueles aqui obtidos: a) teriam as floras pretéritas do Sul da América e norte da Península Antártica, afinidades comparáveis que denunciem a manutenção das conexões terrestres entre estas duas massas de terra do Gondwana, antes do final do Cretáceo? b) podem as paleofloras e suas ferramentas, auxiliar na compreensão dos processos deposicionais e do contexto geológico envolvido nas mudanças paleogeográficas e paleoclimáticas? c) são os dados provenientes das faunas marinhas e aqueles das floras, coerentes no que diz respeito às propostas de variações do clima momentos antes do final do Cretáceo? d) seriam os grupos de fetos identificados, muitos hoje exclusivos das áreas pantropicais do globo, bons análogos para testar as condições de “hot house” propostas para o final do Cretáceo, mesmo nas altas latitudes? e) por sua história evolutiva de sucesso e de permanência no Planeta, qual o significado de sua preferência pelas áreas instáveis submetidas a intenso tectonismo, ainda hoje presentes, por exemplo, na costa do Pacífico e cujas ilhas ainda resguardam suas formas relictuais (Nishida, H. 1984; Mueller-Dombois et al, 1998).

Finalmente, buscaram-se aqui respostas para um tema ainda cercado de incertezas, referente à origem de certos grupos de Pteridófitas. Copeland (1939) sugeriu que as áreas do Gondwana, e em especial da Península Antártica, tiveram um papel importante como centro de origem de diversos grupos de pteridófitas (e.g. Hymenophyllaceae, Cyatheaceae). Considerando o trabalho pioneiro deste pesquisador, a hipótese aqui investigada é se a presença destas floras de pteridófitas suporta esta ideia, e assim, quais teriam sido as possíveis rotas de dispersão deste grupo de plantas e que processos controlaram seus eventos de irradiação.

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**A new cyathealean tree fern from the basal Upper Cretaceous of Livingston Island,
Antarctic Peninsula, and its close relations with the extant *Thyrsopteris elegans*
Kunze**

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Abstract

Sterile and fertile pinnae related with *Thyrsopteris* are described to Cenomanian beds from the volcanic succession of Hanna Point in Livingston Island, South Shetland Islands. They represent the oldest known record of such a kind of tree fern, today included in the Cyatheaceae. Its record gives support to the proposals of an origin to the genus in the insular areas of western Antarctic Peninsula, which dispersion processes were after affected by the maintained plates subduction along the Pacific margin, follows by the Gondwana break up and the resulting environmental changes. The *Thyrsopteris* related remains of Hanna Point (62° of latitude) shows exclusive morphological and reproductive features in relation to previous knowing fossils of the genus, been more next of the unique extant species *T. elegans* Kunze, today growing at Juan Fernández archipelago, in Chile (33°-34° S of latitude). The partially preserved sterile pinna, with a grooved axis, bears acroscopic and dissected pinnules, alternate to sub-opposite disposed, with free veins and rounded lobes. The fertile one exhibit well-defined stalks with an apical clavate receptacle and round to reniform cyatheoide sori. In the fossil assemblage, the dominance of pteridophytes approximates the Hanna Point beds to those of the Early Cretaceous successions of the proper Livingston Island and the nearby Snow Island (Byers Group). However, rare fragmented leaves of angiosperms give support to the younger Cenomanian age informed by the radiometric age data. Scarce and still dubious forms assigned to *Thyrsopteris* are also recorded to Mesozoic and Paleogene floras from South America and Antarctic Peninsula, where warm temperate oceanic climates and a forearc geological context was inferred, in analogous conditions to that today controls the growth of *T. elegans*, its exclusive extant species.

Keywords: *Thyrsopteris*, Cyatheaceae, Upper Cretaceous, Hannah Point, Livingston Island, Antarctic Peninsula

1. Introduction

The scaly tree ferns (Cyatheaales) are today a characteristic component of the understorey in the tropical/subtropical and south temperate plant communities, where are known by their characteristic habit and large compound leaves (Jones et al., 2007; Korall and Pryer, 2014). After a proposed origin and diversification in the Late Triassic of its three major lineages (heterosporous water ferns, tree ferns, and polypods) from the monophyletic leptosporangiate ferns, in a still uncertain area of Australasia or South America (Pryer et al., 2004), the tree ferns show been an important component of the Jurassic to Paleogene worldwide plant assemblages. In this process were included areas of the Antarctic Peninsula, where the Cyatheaceae and Dicksoniaceae are its main representatives (Van Konijnenburg-Van Cittert, 1989; Zhou Zhian and Li Haomin, 1994a, 1994b; Dettmann et al., 1992; Falcon-Lang and Cantrill, 2002; Césari, 2006; Leppe et al., 2007; Vera, 2010, 2015). In the Cretaceous, with the establishment of the Weddell Sea in northern Antarctic Peninsula, fern communities also dominates the deposits of eastern marginal Graham Land and in the Larsen Basin (Gee, 1989; Rees and Cleal, 2004; Birkenmajer and Ociepa, 2008). Until there, forests of typical Mesozoic conifers, with tree ferns, ginkgoaleans, bennettitaleans and pentoxylaleans in the sub-canopy, and liverworts and other ferns in the understory (Schizaeaceae, Gleicheniaceae and Osmundaceae) had covered also the coastal and deltaic areas of the western forearc islands (Philippe et al., 1995; Torres et al., 1997) and still those of southern Patagonia (Schwartz and Graham, 2015).

Was in this kind of community that arriving the first angiosperms in the Albian (Askin, 1990; Spicer et al., 1993; Cantrill and Poole, 2012; Bowman et al., 2014; Nagalingum and Cantrill, 2015). Contrary to other authors consensus, Schneider et al. (2004) shows that the presence of the angiosperms incentives the diversity of certain lineages of ferns, which is well observed in the Paleogene assemblages. However, the new land bridges and high areas created in the circumscription of the volcanic arc was also probably involved in these evolutionary process and in the dispersion of the Cyatheaales to the southern areas of Patagonia and Australasia (Berry, 1922; Menéndez, 1966; Leppe et al., 2007, 2012; Vera, 2009, 2015). The beginning of Cretaceous marks its diversifying and broader distribution, with more secure fossils of Cyatheaceae been also record in areas of South Africa, New Zealand and Tasmania (Couper, 1953;

Tidwell and Ash, 1994; Stockey & Rothwell, 2004; Vera, 2009; 2013; Vera and Herbst, 2015).

To Césari et al. (2001), the presence of the large arborescent ferns since the Mid-Jurassic and in all Cretaceous at the Antarctic Peninsula, confirms the warm temperate conditions of the climate proposed in the pioneer works (Dusén, 1908; Francis, 1986; Dettmann and Thomson, 1987; Askin, 1983, 1992). Attest also their affinity by coastal insular areas influenced by volcanism and humidity, today still maintain by the Cyatheaceae in South America, Tasmania, New Zealand and Malaysia (Holttum, 1963; Tryon and Gastony, 1975; Janssen et al., 2008) and that also controls the growth of the extant *Thyrsopteris elegans* Kunze (Tryon, 1970; Tryon and Tryon, 1982; Stuessy et al., 1990, 2018). Recent works still approached the significant impact of the Gondwana breakup and Andean uplift over the Cyatheales distribution (Dutra, 2004; Antonelli et al., 2009; Korall and Pryer, 2014).

In this work, a new Upper Cretaceous pteridophyte remains are described to Cenomanian levels of the Livingston Island, Antarctic Peninsula (Fig. 1A-B). It was identified at the Hanna Point, in the south-central part of the island and shows sterile and fertile fragments of fronds, which structures indicate an affinity with the Cyatheaceae and the extant species, *Thyrsopteris elegans*. If those relations are confirmed, represents the ancientest until now known for to this species and could contribute to a better understanding of its evolutionary pathways and of its answers to the distinct ecological constraints that influence the geography and the life in the southern high latitudes in a critical moment of the Earth history.

1.1. Cyatheaceae: modern distribution, phylogeny and fossil history

The scaly tree ferns or Cyatheaceae (including *Hymenophyllopsis*) are the largest group of Cyatheales, and one of the eight recognized families in the phylogenetic studies, with Thyrsopteridaceae, Culcitaceae, Loxsomataceae, Plagiogyriaceae, Dicksoniaceae, Cibotiaceae and Metaxyaceae (Kubitzki, 1990; Pryer et al., 2004; Conant et al., 1994, 1996; Smith et al., 2006; Schuettpelz and Pryer, 2007; Christenhusz et al., 2011; Lehtonen, 2011). To Korall et al. (2006) they are a monophyletic group, meanwhile, Lantz et al. (1999) and Pryer et al. (2004), consider this character still uncertain and needing new circumscriptions, is special when the Cyatheaceae and Dicksoniaceae are involved.

When those previous taxonomic and phylogenetic conceptions were analyzed with a special focus on how the tree ferns changed over time, Christenhusz and Chase (2014) propose the inclusion of the above families, as subfamilies of Cyatheaceae. To them, the advantage in this approach is to make possible moved the different genera (still conflicted), without altering the family placement expressed in distinct works, and ever taking into account that, by its long generation time, the tree ferns clade shows minimal genetic divergences. Based in Christenhusz (2009), they also suggest that the helicogyroid annulus in the sporangium is the best diagnostic character of the Cyatheaceae and a synapomorphic feature of all Cyatheales (unfortunate rarely preserved in the fossil record). Recently Cheng and Yang (2017), resume the importance of include fossils in the phylogenetic approaches and still point to the difficult use of the Smith et al. (2006) approach, when the focus is the taxonomic insertion of some cyathealean, especially those of the Cretaceous, and as shown by the *Thyrsopteris* related forms from Antarctica, like the herein described.

Copeland (1947) was the first to suggest an origin of the Cyatheaceae in the Jurassic of Antarctica, a proposal after support by Tidwell and Ash (1994), based in the presence *Oguracaulis* Tidwell, a primitive form identified in the Jurassic of Tasmania and sharing an Antarctic origin (Tidwell et al., 1989). Nevertheless, in the biogeographic approach of Korrall and Pryer (2014), an origin in South America or Australasia and in beginning od Cretaceous was proposed, coinciding with the Cyatheaceae-Dicksoniaceae divergence. To them also, the crow group of Cyatheaceae appeared in the mid-Cretaceous (96 Ma).

After this and to the Paleogene, extensive forests cover the areas between 60°–80° S of latitude, with many fern groups established mainly in the Antarctic Peninsula areas, enjoying the mild and humid climate (Stuessy and Taylor, 1995). The arriving of the angiosperms to the high latitudes still in the lower Cretaceous and the gradual end of the continuous Gondwana landmasses will affect those fern assemblages (Lupia et al., 1999; Berendse and Scheffer, 2009). To Collinson (2004), the modern range of Cyatheales distribution will be only reached in the Neogene, with the fall down of global temperatures and humidity. Today they are represented by more than 660 species growing in tropical areas of Europe and Asia, in Hawaii and Malaysia, and in the cloud forests of the North and South America (including Amazonia). They also grow in restrict warm-temperate areas of southeastern Brazil and northeast Argentina, where are linked to the “Araucaria forests” (Sehnem, A. 1978; Tryon and Tryon, 1982; Weigand

and Lehnert, 2016). To Tryon & Gastony (1975), 210 species of Cyatheaceae harbour near the Neotropics, with centres of endemism in the oceanic islands of the Greater Antilles, southern Mexico and Central and South America. Additionally, in South Hemisphere, they extend its distribution to cool temperate forests of the Antarctic region (Large and Braggins, 2004; Smith, 1993; Ramírez-Barahona et al., 2011), and seem to confirm the role of Antarctica in its geological history (Drinnan and Crane, 1990).

1.2. Extant scaly tree ferns and the endemic *Thyrsopteris elegans* from the Chilean Juan Fernández Archipelago (JFA): geographic distribution and ecological appeals

The modern geography of JFA is controlled by its volcanic origin, generated over a hot spot and/or in the border of a tectonic plaque that along its history, moving eastwards and subducting beneath the South American continent (Baker, 1967). Those constrain allows generate dense tree ferns communities, where *Thyrsopteris elegans* and *Dicksonia berteriana* are the main components over the highlands of the Robinson Crusoe Island (RCI), the next one to the Chile mainland (Greimler et al., 2002).

T. elegans is a scaly tree fern characterized by distinct sterile and fertile pinnae (dimorphic) of adaxial-grooved axes (Tryon and Tryon, 1982) and alternately disposed pinnae (Fig. 2A). The sterile one bears acroscopic, slight asymmetric pinnules of also alternate insertion and lobate margins, supplied by free veins (Fig. 2B-D). In the fertile pinnae, strongly reduced laminas (stalks) originates an apical clavate receptacle, each one bearing round to reniform sori of cup-shape (cyatheoide) indusium (Fig. 2E-G), that to Korall et al. (2006) characterizes an apomorphic character.

Forest stands with *T. elegans* and *D. berteriana* had been used as a criterion for delimiting the upper (700- 1200 m) and dryer montane forest of the southern part of the island (Skottsberg, 1953a; Stuessy et al., 1998; Greimler et al., 2013). Despite its unique eco-region character, with endemic plants slowly evolved, if other components of the JFA flora are included, this biome shows share an extraordinary range of geographic affinities, extended since the Andes and sub-Antarctic Patagonia, to Hawaii-Tahiti and New Zealand (Carlquist 1980; Mueller-Dombois and Fosberg 1998).

In New Zealand, the Cyatheaceae and Dicksoniaceae can represent more than 50% of the basal area and 20% of the forest biomass. Brock et al. (2016), in a review of

the ecology and significance of the tree ferns in those forests structure, considered it a model of other southern wet temperate rainforests, growing in coastal areas of South Hemisphere and in areas between 30 to 45°S of latitude. To Shester (2008), this location and the distance from the continent, make that subtropical waters reach JFA, moderating the influence of the sub-Antarctic Humbolt cold current. To him, it results in a unique seasonal climate, with warm temperate dry summers (18.7° C in average) and cooler wet winters (7.3° C of temperature and 1.041,5 mm of humidity). In the low lands and at its higher southern mountains, often hidden by clouds and under a 10°C of average temperature, the contrasting climate parameters are softened by the near coastal humidity (Skottsberg, 1953b; Hajek and Espinoza, 1987; Novoa et al., 1989; Greimler et al., 2002). Solitary, or with other ferns, *T. elegans* dominates the forested soils of the upper mountains in RCI, where grow over an often-thick organic layer that, together with abundant bryophytes forms a dense cover, usually reaching 3 m in height (Greimler et al 2002). They are rare, however, in the similar stands of the neighbour Alejandro Selkirk Island, where *Lophosoria quadripinnata* dominates (Greimler et al., 2013).

1.3. Morphological and reproductive features of *Thyrsopteris* related fossils, past distribution and the difficulties in its taxonomic insertion

Nowadays, *Thyrsopteris* is represented by the unique species, *T. elegans* Kunze (Fig. 2), and so a potential analogous to similar forms found in the fossil record. Their endemic character and its important role in JFA flora were pointed by many authors (e.g. Bower, 1926; Tryon and Tryon, 1982; Stuessy *et al.*, 2018). *T. elegans* is also unique among living pteridophytes in associate an arborescent habit with dimorphic fronds of grooved axes and anadromic branching. The fertile frond bears stalked sori, more or less transversely oriented, and insert on a clavate receptacle with cyathiform (cup-shape) indusium (Van Konijnenburg-Van Cittert, 1989; Friss and Pedersen, 1990). However, the molecular studies attests the weakly based relations of *Thyrsopteris* with other arborescent ferns (Korrall *et al.*, 2006; Smith, 1993; Christenhusz *et al.*, 2011) and incentives the recent proposal of its inclusion in the Cyatheaceae Family, together with *Dicksonia*, *Cibotium*, *Cyathea*, *Plagiogyria*, *Loxsoma* and *Culcita* (Rothfels *et al.*, 2012; Christenhusz and Chase, 2014).

The generic and specific assignment of the modern *Thyrsopteris* is due to Kunze (1834), from samples collected by C.G. Bertero (1830) in the Juan Fernández Island. Hooker (1844, 1846), that previously included the same material in *Dicksonia*, yet accepted this new generic insertion, maintain *Thyrsopteris* in the Dicksoniaceae and in Cyatheae tribe (Hooker & Baker, 1874, p. 16, Tab. 1, fig. 3). Diels (*in* Engler and Prantl, 1924) and Bower (1926), convinced about a more proper inclusion in the Cyatheaceae, established the new tribe Thyrsopterideae for includes the genus, calling the attention to its transitional character between *Dicksonia* and *Cyathea*. Based in Seward (1913) he pointed out to the similarity between the extant *T. elegans* and some Jurassic morphotypes found in Yorkshire, considering it a survivor of the Mesozoic forms. Moreover, Copeland (1939), which also highlight the relictual condition of the modern species and the mixed features present in *Thyrsopteris*, considered it a good portrait of the probable common ancestor of *Dicksonia* and *Cyathea*. To him, the presence of hairs in the stems, and the transversally disposed sori approximates the genus of the Dicksoniaceae, meanwhile, the cupulate sorus is common to the Cyatheaceae. To Van Konijnenburg-Van Cittert (1989), also in agreement with this mélange of characters, the presence of a cup-shaped indusium could be a good tool in distinguishing the Thyrsopterideae subfamily from the bivalve ones of the Dicksonieae.

Those aspects were critical in the study of fossils restricted to sterile frond, which sharing features with another coeval genus (e.g. *Onychiopsis*, *Dicksonia* and *Coniopteris*), or with assemblages that include only permineralized stems or spore grains. It was probably the reason why Berry (1911), when revised the Early Cretaceous material from North Hemisphere Potomac flora, linked to *Coniopteris*, forms originally considered in *Thyrsopteris* by Fontaine (1889). After treating with the Upper Cretaceous and Eocene materials of Patagonia, Berry (1938) adopted the same posture, leading to the critical revision made by Kurtz (1902) and Hünicken (1971). Harris (1961), working with what was considered Dicksoniaceae in Yorkshire levels, highlighted the expressive presence of the Thyrsopteroideae subfamily (with eight species) in relation to that of the Dicksonioideae (two species) and suggests that a continuum between the sorus annulus and the stalk, and “robust valves”, discriminate the Dicksoniaceae. By the similar sort of *Coniopteris hymenophylloides* and *T. elegans*, he encloses them in the first genus (and those of *Eboracia*) in the Thyrsopterideae subfamily, a condition also adopted by Van Konijnenburg-van Cittert (1989), when works with the same Yorkshire flora.

In the Gondwana, macrofossils related with the Cyatheaceae are characteristic in the Cretaceous, mainly on areas of the paleo-Pacific margins of the Antarctic Peninsula. There the family (including *Thyrsopteris*) is nearly exclusive from the forearc western islands (Figure 1A, Table 1) and mainly to the Aptian assemblages of Cerro Negro Formation, Byers Peninsula, where dominates the pteridoflora and represents up to 6% of the total assemblage (Césari et al, 1999, 2001; Vera, 2009; Falcon-Lang and Cantrill, 2002; Parica et al., 2007). It surpasses the 2% of representation identified in levels of the same age in the Baqueró Group, South Argentina (Vera, 2010, 2015), and those from the Chilean Magallanes Basin (Menéndez, 1972; Hervé et al., 1981).

Some other scarce remains, accompanied by spore grains of *Cyathidites minor* Couper were also identified in Campanian levels of the Rip Point, Nelson Island (together with *Coniopteris* related fronds), and at Fildes Peninsula, in southern King George islands (Cao Liu, 1994; Dutra and Batten, 2000, see also Table 1). In Australia, Nagalingum *et al.* (2002) observe a decline of the Cyatheaceae/Dicksoniaceae (16-22% to 10%), between the Early and Late Cretaceous. Other evidence about the presence of Cyatheaceae in South Hemisphere basins is scarce, the exception being the Cretaceous permineralized frond axes from Eastern China, Japan and Southeastern Africa.

Thyrsopteris will be maintained in the South Shetlands Islands to at least the beginning of Eocene, represented by the well- preserved fertile and sterile fronds of *T. shenii* (Zhou Zhian & Li Haomin, 1994a), and by the dubious spores of *Cyathidites* (Torres & Méon, 1990) and permineralized stems (Torres, 1990).

Similar difficult taxonomic conditions surround the discrimination of the *Thyrsopteris* related spore grains. In the Antarctic Peninsula and in other austral basins, many forms of, for example, *Cyathidites*, were found and shares common structural features (Table 1). Still dubious in its familiar and generic affinities (Shuklina and Polevova, 2007; Vera, 2015), *Cyathidites* comprise a broad category (Balme, 1995), been recognized by also possible links with the Dicksoniaceae and Schizaeaceae (Raine et al., 2011). Copeland (1947) and Couper (1953), when described *Cyathidites australis* from New Zealand, call the attention to the shared size (50-(55)-70 μ) and globose form, with spore grains of both Dicksoniaceae and Cyatheaceae, and with those of *T. elegans*. Moreover, many authors highlight that, despite *C. australis* can be linked with the Cyatheaceae, shows also affinities with the spores of *Cladophlebis*, a common component of the Cretaceous fossil record (Couper, 1953; Harris, 1961, Tryon and Tryon, 1982; Kubitzki, 1990; Tryon and Lugardon, 1991). To *Cyathidites minor*, Raine

et al. (2011) propose a relation with the modern *Cyathea* and *Thyrsopteris* genera (and also, with *Eboracia lobifolia*, *Coniopteris hymenophylloides* and *Dicksonia mariopteris*).

By the scarce presence of *Cyathea* in southwestern Gondwana and Patagonia (Heusser, 1971; Morbelli, 1980), we include the record of *C. minor* in the tabulated data (Table 1) about *Thyrsopteris* past occurrence, until more secure relations with the genus were proposed. Despite the absence of spore grains in the material from Hanna Point, our goal was to test their conjunct occurrence with more secure related fronds or wood remains of *Thyrsopteris* in the fossil assemblages of the Antarctic Peninsula, and so looking for inferences about its affinities and dispersion routes.

In the detailed analysis of Gastony (1981, 1982) about the link between *Thyrsopteris* and *Cyathidites*, they proved that the spores grains of modern *Thyrsopteris* are distinct from those of *Cystodium*, *Cibotium*, and *Dicksonia*. Christenhusz and Chase (2014), based on the pioneering proposal of Holttum (1963) assume a relation between *Cyathidites* s.l. and the Cyatheaceae, meanwhile *Cyatheacidites* have a close relation with *Lophosoria quadripinata* C. Chr., as previously proposed by Dettmann (1986) and Raine et al., 2011).

The inventory herein made shows that more secure relation between *Cyathidites* and *Thyrsopteris* comes from the K-Pg levels of the Antarctic Peninsula, by their conjunct occurrence with permineralized stems and frond impressions (Table 1). Since rare in the pteridophytes palynofloras dominate by Gleicheniaceae and Adiantaceae, *C. minor* was part of assemblages (with fungi, bryophytes, conifers and few angiosperms), which analogous grows today in oceanic islands of Tasmania, New Zealand and southern Chile (Ponce *et al.*, 2002; Cantrill & Poole, 2012). The *Thyrsopteris* and other Cyatheaceae related spore grains are however absent from the Mesozoic backarc deposits of eastern Antarctic Peninsula (Gee, 1989; Hathway, 2000; Riding and Crame, 2002) and those from southern South America. In the last area, however, "*Dicksonia*" *patagonica* Berry 1938, a dimorphic frond identified to the Eocene of Rio Pichileufú, Argentina, shares common features with *Thyrsopteris*. The rarity of Cyatheaceae in the backarc basins could result from it distinct environmental context, with low atmospheric humidity and distance of the open ocean. Their occurrence in the K-Pg boundary deposits of Seymour Island (Askin, 1990), seemly reflect the first seawater invasions resulting from the establishment of the Weddell Sea.

2. Geological setting

As part of the South Shetland archipelago, Livingston Island is inserted in a forearc context similar that seen to the modern JFA, and that controls all the NW Antarctic Peninsula deposits, largely also dependent on of the magmatic arc evolution and subduction processes of the Pacific oceanic crust (Barker, 1982; Barker et al., 1990; Elliot, 1991; Bastias *et al.* 2016). By those constraints, the South Shetland is a well-exposed example of a long-lived volcanic arc, maintained active between 135 Ma to c. 24 Ma (Haase et al., 2012). In the Late Cretaceous, it was also strongly affected by the fault systems of the gradual Gondwana breakup (Smellie et al., 1984; McLoughlin, 2001; Livermore et al., 2005; Hervé et al. 2006; Reguero et al., 2013). Many authors, however, consider that a continental area persists between southern South America/northern Antarctic Peninsula until 84 Ma, and that the western areas of the Scotia Sea were maintained together until the Paleogene (Cunningham et al. 1995; Lawver and Gahagan, 1998, 2003; Ghiglione et al., 2008; Eagles, 2010). The definitive isolation of the Gondwana landmasses at the end of Eocene (Drake Passage) and the resulting drop of global temperatures and atmospheric CO₂ concentrations, will sharply imply over its terrestrial life (Anderson et al., 2011; Zachos et al., 2001).

Resulting from this complex tectonic genesis, pyroclastic rocks dominate the South Shetland Islands successions, with rare intercalated fluvial and lacustrine epiclastic deposits (Smellie et al., 1984; Birkenmajer, 2001; Haase et al., 2012). The last body water deposits concentrate the fossil leaf impressions (Askin, 1983; Dutra, 2004; Cantrill and Poole, 2012), meanwhile permineralized fossil woods or stems occurs in pebble-boulder conglomerates, volcanic breccias or still on lava flows, were are represented by charcoalfied materials (Phillipe et al., 1993; Torres, 1993; Poole and Cantrill, 2006; Falcon-Lang and Cantrill, 2002; Manfroi et al., 2015). To Birkenmajer et al. (1986), the additional influence of a hotspot system explains the in part observed younger ages of the floral assemblages, from the south (Cantrill and Nichols, 1996) to northern islands (Dutra and Batten, 2000). However, to Pankhurst & Smellie (1983) and Haase et al. (2012), this asynchrony must better reflect an SW-NE migration of the volcanism in the island arc subduction (to Haase et al., 2012, in a single island scale), between the Jurassic and basal Eocene.

Livingston is the second largest island of the South Shetland Archipelago and the source of the Hanna Point pteridophytes herein presented. Other four areas are

known for its content of plant fossils, with ages varying between Triassic and Upper Cretaceous (Fig. 1B). At Hanna, a succession of basaltic andesitic to dacite lavas and breccia (the Younger Volcanic Group of Hobbs, 1968) shows interbedded pyroclastic and thin epiclastic levels affected by block dislodgement and crustal contamination, which difficult the age assignments (Smellie *et al.*, 1984, 1996; Pallàs *et al.*, 1999; Bastias *et al.*, 2016). The obtained data indicate distinct magma sources and two Upper Cretaceous intrusive episodes, the first in the Cenomanian (affecting the unit E of Pallàs *et al.*, 1999), and the second in the Coniacian-Santonian (Smellie *et al.*, 1996; Xiangshen *et al.*, 1996; Haase *et al.*, 2012). Between other aspects herein presented, including the age, it distinguishes the deposits from Hanna Point from the Aptian ones of President Head, Snow Island, and the abundant ones from Byers Peninsula and Cape Shirreff, where the Cyatheaceae are also important components (but without *Thyrsopteris*). However, by the occurrence of primitive angiosperms (Leppe *et al.*, 2007), Hanna Point approximates to the Cretaceous deposits of Williams Point (Rees and Smellie, 1989; Torres and Lemoigne, 1989; Phillippe *et al.*, 1993; Poole and Cantrill, 2001).

In 2007, an exceptionally warm summer allows exposed new plant fossils (Fig. 3), in levels which correspond to the lower Unit D of Pallàs *et al.* (1999). Identified by Leppe *et al.* (2007), they are part of a 110 m thick pile of agglomerates, ashes and amygdaloidal lavas, inserted between massive andesites, and interbedded with green agglomerates, amygdaloidal lavas and tuffs (Hobbs, 1968). In the 25 m thick of the newly Hanna Point exposition, the plant fossils occur in two levels, the upper composed by tuffaceous layers and the lower by fine-grained volcanoclastics (Fig. 4). The first is characterized by exclusive conifer leaves (*Elatocladus* and *Pagiophyllum* podocarps) and recovers the volcanoclastic lithologies containing the dominant pteridophytes flora, accompanied by gymnosperms (*Ptilophyllum*, *Elatocladus*, *Podozamites* cf. *P. binatus* and *Brachyphyllum*), a dubious pteridosperms seed cone (*Pachypteris?*) and fragments of angiosperm leaves (linked to *Nothofagus* and other dubious remains), previously informed and illustrate by Leppe *et al.* (2007). Conifer woods, related with *Agathoxylon* and *Podocarpoxylon*, occurs in the lowermost volcanic breccia and conglomerates and was described by Torres *et al.* (2015).

Leppe *et al.* (2007) considered that the fern assemblage was composed by Osmundaceae, Dicksoniaceae and Gleicheniaceae (*Adiantites*, *Matonia*, *Gleicheniaceaphyllum*, *Microphylopteris*, *Coniopteris* and *Sphenopteris*) and by two

species of *Cladophlebis* (*C. antarctica* and *C. oblonga*), and illustrate the first occurrence of a *Thyrsopteris elegans* related fossil to the island, the form herein described. Except by the still dubious presence of flowering plants, the assemblage is not so distinct from those characterizes other Upper Jurassic-Early Cretaceous levels from the Antarctic Peninsula areas (Gee, 1989), mainly those from the proper South Shetland Islands (Cantrill and Hunter, 2005; Nagalingum and Cantrill, 2006; Cantrill and Poole, 2012).

3. Material and methods

The 52 total samples analyzed were collected by the Chilean Antarctic Institute team (INACH) in the summer season of 2007. Between them, the pteridophytes represent 70% of the components and are preserved by imprints of fragmentary fronds and rachis. The herein described form is the unique referring to *Thyrsopteris* and, despite its partial preservation due to the unfavourable sand-size grains of the lithologies, exhibit some organic fine details. The conjunct occurrence of a fertile frond (without organic connections) incentives its descriptions.

An Olympus SZH10 stereo microscope, with a drawing attached device was used in the analysis of morphological appeals, after record with a Canon DSLR EOS digital camera using both polarised light and filters to enhance contrast, or low-angle lighting to reveal surface details. Fine features were also drawing over the photos, using Adobe Illustrator CC. All fossil remains were lodge within the Paleontological Collection of Antarctic and Patagonia from INACH and have been assigned to CPAP archive numbers.

To discriminate affinities with extant *T. elegans* Kunze, frond exsiccates stored in the Herbarium leaves 21-24, of the Muséum National d'Histoire Naturelle (MNHN) from Paris were used (Fig. 2A–E and 5G). They refer to the type material described by Gustavo Kunze in 1834, based in samples collected in 1830 by Carlo Bertero, at Juan Fernández island. Originated from the same island and from the Bertero collects are also materials (Fig.2F), stored in the Royal Botanic Garden of Edinburgh herbarium (see Fig. 2 to the source addresses). However, the more complete and well-record and illustrated MNHN samples was preferably used in the comparisons. Finally, exsiccates referring to *T. elegans* (sample no. 16626) from the Botanical Department of Concepción University (CONC-UDEC), in Chile, was also analysed.

In the describing and comparisons with the scarce fossil material related with *Thyrsopteris* pinnae, forms recorded to the South Hemisphere were analyzed. They attest an exclusive occurrence in deposits of the Antarctic Peninsula and South America, where are accompanied by distinct species of *Cyathidites* spores (see Table 1). One of them refers to the holotype of *Thyropteris antiqua* Menendez (sample BAPB 8100), from the Upper Cretaceous of Cerro Guido, southern Chile (Menéndez, 1966), kept in the paleobotanical collection of the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina. It was there analysed and photographically recorded (Fig. 5E–H). Other specimens refers to the fertile and sterile fronds of *Thyrsopteris shenii* Zhou and Li (holotype PB 15450), from the Lower Eocene of King George Island, Antarctic Peninsula. The analyses were made through the well-illustrated samples of the original work of Zhou Zhian and Li Haomin (1994a, Pl. 2, figs. 1–7a and 10; Pl. 4, figs. 1–6; Pl. 5, figs. 3–3a). Other related fronds, as some of those included in *Culcita*, *Coniopteris* and *Onychiosis* genus, described to South Shetland Islands, Hope Bay, Seymour Island, and Patagonia (Table 1), was compared by its original diagnosis and illustrations in the literature, looking for sharing and distinct features.

The taxonomic insertion was base in the proposals of Korall et al. (2006), Smith et al. (2006), and Cristenhusz and Chase (2014). An analysis looking for associated spore grains shows unfertile materials.

4. Systematic Palaeontology

Class Polyopodiopsida
Order Cyatheales A.B. Frank
Family Cyatheaceae Kaulf
Subfamily Thyrsopteridoideae B.K.Nayar
Genero *Thyrsopteris* Kunze

Type species *Thyrsopteris elegans* Kunze 1834

Thyrsopteris elegantiforma nov. sp. Trevisan and Dutra
(Figure 5A–D)

Etymology. The specific epithet reports to the next morphological features between the fossil and the extant *T. elegans*.

Type specimens. CPAP 2408 referring to a partially preserved sterile pinna; CPAP 2358, mould and cast of a pinna, with fertile pinnules.

Other materials. CPAP 2381, ultimate sterile pinna; CPAP 2360a/ 2360b, mould and cast of fertile pinnae.

Diagnosis. Dimorphic frond with adaxial grooved axes. Sterile pinna acroscopic inserted, bearing alternate disposed of asymmetric and lanceolate pinnules, deeply dissected, with decurrent constricted bases and round apices, thick texture and revolute margins. Pinnules 5-7 lobate, with lobes more developed in the anadromic side, the basal one bigger and deep dissected and parallelly orientated in relation to the rachis. Each pinnule is supplied by one main vein sometimes bifurcate at the base (dichopodial) with an in general basisopic course. From that two to five upward branches diverges, ending in the margin lobes. Fertile pinnules of strongly reduced laminae (stalk), also alternately disposed of, the proximal ones once or twice dichotomized. Each apical clavate receptacle bears a unique round to reniform sori of cyathiform indusium.

Description. The sterile fragments of pinnae show stout and grooved rachis (1 mm wide) and vary between 5–6 cm long and 1, 52 cm wide. The up to 15 alternate to subopposite asymmetric pinnules, arranged in angles of 20°–40° (1 cm of length), exhibit decurrent bases and lobate margins, apically reducing in size and number. A more developed basal, acroscopic pinnule lobe, accompany all the extension of rachis, parallelly orientated. The weakly preserved vein pattern shows a single basal costa per pinnule, accompanying the catadromic margin. The fertile pinnule (20 mm long, 10 mm wide) bear five to ten globose/reniform sorus of cup-shape indusium (1,7 mm in diameter), one per stalk and apically inserted, the proximal ones in general forked.

Comparisons. The gross morphology of the isolate ultimate pinnae identified in Hanna assemblage, by it inferred dimorphic frond with the grooved axis, decussate and lobate pinnules with anadromous-branched veins, accompanied by fertile pinnules with cup-like sporangia, approximate the Hanna Point sample from that of the Cyatheaaceae and of *Thyrsopteris elegans*. The following comparisons take this into account, and besides the modern form, look for similar features in the scarce materials assigned to the genus in fossil assemblages of the South Hemisphere. Other similar types (from North Hemisphere), or those included in other fern families or genera were only briefly addressed (see also Table 1).

In the fossil record, the currently considered ancientest *Thyrsopteris* related form had been identifying in the Maastrichtian levels of the Cerro Guido, in Chilean

Patagonia. It refers to the associate sterile and fertile fronds, described by Menéndez (1966, Lamina 1) and assigned to the new species *T. antiqua*. In the synonym of the new species, he includes forms considered by Kurtz (1902) and Hünicken (1971, figs. 3-4) in *Asplenium dicksonianum* Heer. The revision here made with the Menéndez holotype (Fig. 5E-H) shows that, despite the dimorphic frond with alternate and acrodromous pinnules, and the cup-shaped sori, *T. antiqua* differs from extant *T. elegans*, and the form herein described, by the high-dissected elongate and triangular sterile pinnules, with narrow angles of attachment (5° – 10°) and dentate lobes. By this pinnule morphology, *T. antiqua* approximates better to the foliages described to the north-hemisphere Potomac Group by Fontaine (1889), and mainly to that assigned to *T. insignis* Fontaine (Pl. XLII, Figs. 1–4). As seen herein, most of the Potomac materials were after included in *Coniopteris* or *Onychiopsis*, but in each manner, such morphological features are uncommon in the Cyatheaceae, and normally includes in the Dicksoniaceae. Moreover, *T. antiqua* shows a thinner rachis and no mention is made to the presence of a groove in the axes of the chosen holotype of Menéndez (1966). In relation to the fertile pinna, considered by the author linked to the sterile ones yet the connection zone is weakly preserved, *T. antiqua* is also distinct by the superimposed and disorganized sori (a spike?) and by its broader and short laminar stalk (Menéndez, 1966, Fig. 1).

Another comparable dimorphic fronds are that identified by Berry (1938, Pl. 7) to the Eocene of Pichileufú River, in Argentina, and included in the new species *Dicksonia patagonica*. By its gross morphology (alternate pinnules of the decurrent base and lobate margins, number of lobes and the well-developed acroscopic lobe), *D. patagonica* is too next from the here described materials. However, a kind of uncertainty is maintained in relation to the presence of a grooved axis (no comments about it is given in the diagnosis), and mainly by the presence of a bivalved indusium. Despite this, and the generic epithet chosen, Berry (1938) consider it related with the Cyatheaceae and with *Cibotium* (yet the monomorphic fronds of the genus), based in the unequal development of the pinnules. “*D.*” *patagonica* and *T. elegantiforma* show also similar sterile pinnules of alternate insertion, decurrent base and lobate margins, with a similar number of lobes. By attests, a presence of a probable *Thyrsopteris* related form in the Cenozoic of the foreland basins of Argentina, “*Dicksonia*” *patagonica* deserves new collects, looking to confirm its preferable familiar affinities. Zhou Zhian and Li Haomin (1994a), working with the basal Eocene of King George Island, also

compare the sterile organs of *D. patagonica* with those of *Thyrsopteris* also call the attention with the sharing features

The new species described by them; *Thyrsopteris shenii* (Zhou Zhian and Li Haomin, 1994a, p. 183 pl. 2, figs. 1-7), are that shares a more next relation in the fossil record with *T. elegantiforma* and with the alive *T. elegans*. The similarities are expressed by the stout rachis, the acroscopic inserted asymmetrical pinnules with decurrent base and acute to round apices, in the ramified anadromic venation and its dichopodially character. The only distinct characters are the nearly entire margins, but such kind of diversified morphology is common also in the more apical pinnae *T. elegans*, (see Fig. 2B). In the fertile pinnules, *T. shenii* and the here described form instead of shares a cyathiform indusium, a number of sori and thinner stalk, has only dubious in its relations in what respect to the presence of a clavate receptacle in *T. shenii*. Unfortunately, one more time in common with Livingston materials, there are no secure organic links between the fertile and sterile fronds of *T. shenii*. However, taking into account the similar morphology and organs arrangement of the fertile and sterile pinnae Zhou Zhian and Li Haomin (1994a), considered that both represent the same individual.

A positive aspect of the Zhou and Li materials is the associate presence of spore grains, considered by the authors relate with *Deltoidospora*, *Cyathidites* and some dubious grains associate to the *Coniopteris* genus (Table 1). The last ones, recognized by its fine ornamented perispore and smooth exospore, weakly developed margo and by the absence of distal and equatorial ridges (similar to those in *T. elegans*), attests both cyatheaceous and dicksoniaceous affinities (Van Konijnenburg-Van Cittert, 1989; Dettman et al., 1992). Cao Liu (1994), after analyzing Late Cretaceous levels of the nearby locality of Half Three Point, in the same King George Island, and Trevisan et al. (2011), working at Rip Point, at the north of Nelson Island, also identify numerous *Cyathidites* related spore grains (Table 1).

Still, other pinnae fragments identified in Antarctic Peninsula areas and restrict to sterile fronds exhibit morphological features similar to those characterizes both *T. elegantiforma* and *T. shenii*. This is the case of *Asplenium antarcticum* Dusén from the Eocene levels of the King George Island (Czajkowski and Rösler, 1986, Pl; IV, Figs. 23-28; Zastawniak, 1981, Pl.1, fig. 2) after associates to cf. *Thyrsopteris elegans* (Dutra and Batten, 2000). Also pinnae fragments illustrate by Zastawniak (1981), from Eocene levels of Point Hennequin Formation (King George) and those of Case (1988, figs. 3B

and 3C), of the Paleocene Sobral Formation, Seymour Island, by its asymmetric ultimate pinnules, seems to be identical to those of *T. elegantiforma* (and *T. shenii*). Levels of the same place and age furnishes also *Sphenopteris angustiloba* (Dusén) Cantrill, Tosolini & Francis (Dusén, 1908, Tab. 4; Cantrill et al., 2011, Fig. 2A–D, I), but only the form of Fig.2 of Cantrill et al. (2011), by the presence of lobate pinnules of decurrent base, is next of the *Thyrsopteris* fossil species.

The analysis made makes clear that mixed features could be present and shared between both Cyatheaceae and Dicksoniaceae. However, at the same time *T. elegantiforma* nov. sp., by its clavate receptacle and cup-shape indusium, confirms a preferable relation with the Cyatheaceae and is until now, and together with *T. shenii*, the closest forms of the extant *T. elegans*. Both link the clearly adaxial grooved axis and dimorphic pinnae (a feature not exclusive of the Thyrsopteroidea), pinnules of similar disposition and morphology, comparable venation appears (main vein acroscopically ramified in free lateral veins) and similar sori, with cyathiform-like indusium, apically inserted in a slender veined stalk.

5. Final remarks

The jointed information attests to the role of the Cyatheaceae in the Cretaceous forests of the Antarctic Peninsula, and mainly to those grown in the insular areas of the Pacific flank. In which relates to the presence of Cyatheales and *Thyrsopteris* in the Cretaceous of Southern Hemisphere, the data expressed in Table 1, showed that 68 % of the remains (pinnae, stems and spore grains) comes from South Shetland Islands deposits, followed by those from Southern Chile (12%), New Zealand and Africa (6% each one) and Argentina (4.4 %).

In those environmental inferences were probably involved the wet climates and mild temperatures that characterized the Late Cretaceous–Eocene times at the high latitudes (8–15°C, to Askin, 1992 and Cantrill, 1998; 7.7 and 23°, to Vera, 2015), although marked by diverse short and episodic intervals of cold in the end of Campanian and along the Maastrichtian (Zachos et al., 2001; Bowman et al. 2014; Brock et al., 2016). Additionally, is important the affinity of the Cyatheaceae with volcanic soils, and its rapid answer to temperature oscillations and environmental disturbances, like lava flows and landslides (Arens and Sánchez Baracaldo, 1998; Woods, 2002; Antonelli et al., 2009). Recent data shows that some groups of Cyatheaceae also can grow in xerophytic areas, like those found in mountains high

heats and forested areas damaged by ice storms, hurricanes, burning or logging (Walker et al., 1996; Barson, 1997).

For another side, the Cyatheaceae (including *Thyrsopteris* and *Dicksonia*) are absent or rarer in the interior continental areas, as for example in Argentina, Australia and Africa, despite they are considered centres of pteridophytes diversity (Moran, 1996; Ponce et al., 2002). This could be probably the cause of the disappearing of most scaly tree ferns, and more drastically of *Thyrsopteris*, on the post- Eocene paleofloras and in those influenced by the Andean uplift, by its rain-shadow context (Table 1). Those constraints can also help in understand its more recently surprising reappearance in contexts very similar to that conditionate it grows in the K-Pg. In spite to prevent the comprehension of its dispersal routes, this behaviour allows new tools about its nowadays-endemic behaviour of the genus.

The closest morphological and reproductive appeals between the fossil and modern *Thyrsopteris*, and the similar ecological strategies here observed are also in accord with the observed trend of the Cyatheaceae towards niche conservatism (tested by Bystriakova et al., 2011), and the minimal genetic divergences of the tree ferns clade (Christenhusz and Chase, 2014). The comparable data between the fossils and extant genera of Cyatheaceae seems to support their almost unchanged condition by at least nearly 100 million years. The massive presence of the family on the insular areas of the Antarctic Peninsula, confirms that mild climates and marginal marine environments existed in those areas since the end of Jurassic, here confirmed by the conjunct occurrence of acritarch, foraminifers and *Cyathidites* spore grains in the same beds (Gee, 1989; Bastos et al., 2012; Bowman et al., 2014).

The occurrence of *Thyrsopteris* in Late Cretaceous and Eocene beds of Antarctic Peninsula, allows proposes that the modern species can be a useful analogous in the study of the fossil-related materials and attests that similar environmental conditions to those today control the JFA area, were present in the insular areas of Antarctic Peninsula in this time interval. It is reinforced, when we include the Aptian floras of Livingston Island, which also shows dominant cyatheaceous fern components. To Brock et al. (2016), the conjunct presence of fungi, bryophytes (Cao Liu, 1994), and podocarp/araucarian conifers (Dutra, 2004; Dutra and Batten, 2000; Cantrill and Poole, 2012), in the Cretaceous assemblages of Livingston and other South Shetland Islands, also make it truly similar to those today occurs in islands from Australia, New Zealand and Chile (Poole et al., 2003; Wiser et al., 2011).

In terms of age, the Cenomanian flora of Hanna Point is too distinct from that of the Aptian Cerro Negro Formation (Byers Peninsula, Livingston Island), and that from the northern Snow Island, and all are also distinct from those identified in the Albian levels of Alexander Island. Additionally, meanwhile ferns represent 39% of the ancient forests of Alexander; they fall to 28% of representation in the younger levels of Hanna. The angiosperms, absent from the Aptian Cerro Negro Formation, appear and represents 12% of the flora in the Albian levels of Alexander (Falcon Lang and Cantrill, 2002).

The here addressed record of *Thyrsopteris elegantisforma* nov. sp. in Cenomanian rocks make of it the oldest known to the genus. In other Cretaceous deposits (New Zealand, Snow Island and Byers Peninsula), forms related with the Cyatheaceae are restricted to spore grains of *Cyathidites minor* and so not truly assumed in its relation with *Thyrsopteris* and the real growth in those areas. If such relations to be confirmed, still oldest records could exist in the southern areas, supporting an Early Cretaceous age and the areas of the South Shetland, as the probable time and centre of origin of the genus.

Moreover, with the proposed invalidity of *T. antiqua* Menendez from the Upper Cretaceous of Cerro Guido, the fossil record of *Thyrsopteris* became restricted to those in Antarctic Peninsula areas. Additionally, Antarctic areas show its maintenance until the beginning of the Eocene, represented by stems, spore grains and fronds (Torres, 1990; Zhou Zian and Li Haomin, 1994a; Dutra and Batten, 2000), confirming its growing. The record of *Thyrsopteris* in the northern tip of Antarctic Peninsula and its absence in southernmost Chile in the Cretaceous times are at least astonishing, and probably in accord with the proposal of Cunningham et al. (1995), about the end of the links between South America and Antarctic Peninsula. To them, more than a gradual loss of land connections, initiate at 80 Ma years, was each time strongest eastward movement of the northern tip of Antarctic Peninsula in relation to South America that interrupts the interchange of organisms. To the authors, a near 500 km of N-S distances separated those two landmasses at 30 Ma, definitively dissolving the possible land bridges.

The similarity between extant *T. elegans* and the new Cretaceous species here described, support its relictual character and evolutionary stasis, similar to that observed by Phipps et al. (1998), with the Triassic Osmundaceae of the Antarctic areas, making it a good analogous to ecological and environmental inference. By the temporal distance between them, however, lead to propose a new fossil species, taking into account not only the IBC Code (Article 1.2), but also the work of Testo and Sundae (2016), which

show that extinctions events occur each 770 thousand years in the Cyatheaceae. The presence of *T. elegantiforma* in basal Late Cretaceous beds of Livingston Island attest its importance, not only to the paleoclimatic and paleoecological reconstructions but also, in recognized its endemic character and the probable origin of the Cyatheaceae crown group at these time interval, in areas of Western Antarctic Peninsula, as inferred by many researchers. The warm temperate climate, insular context and disturbed volcanic soils at the high mountains of the Juan Fernández archipelago, that today controls the growth of *T. elegans* and other tree ferns, are a good analogous to that generates the Hanna Point assemblage.

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Figures and captions

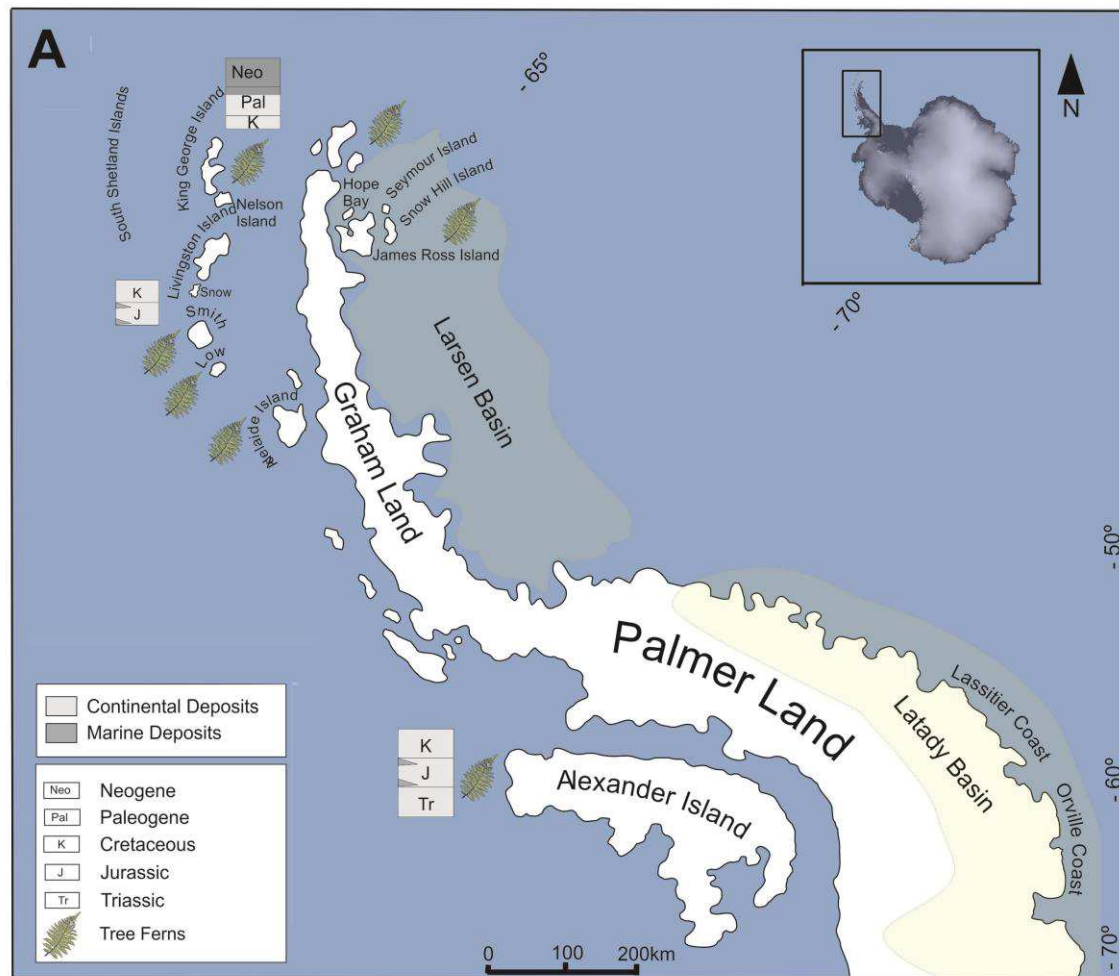


Figure 1. A. Map of the northern Antarctic Peninsula and the location of the South Shetland Islands and the proposed age to the geological units and plant assemblages (from Elliot, 1991);



Figure 1. B. Livingston Island and the main places knowing by plant fossil deposits, with its time insertion based on the isotopic data (^{40}Ar – ^{39}Ar) from Haase et al. (2012). The black rectangle highlight the Hanna Point, the source of the new fossils herein analysed.



Figure 2. Holotype of extant *Thyrsopteris elegans* Kunze from the Robinson Crusoe Island, Juan Fernández Archipelago. **A.** Part of a frond showing distinct sterile and fertile fronds and the grooved axes. **B.** The dissected apical sterile pinna and its asymmetric lobate pinnules, of basal dichopodially venation; **C.** Detail of a lobate pinnule showing lobes supplied by a free vein diverging from the main one; **D.** Sterile

basal pinnae and its pinnule arrangement, highlighting the well-developed acroscopic lobe, parallel orientated in relation to the secondary rachis; **E.** Fertile pinnae detail showing the sinuous and grooved axes and slender stalks with an exclusive apical sori; **F.** Part of a matured fertile pinnae to highlight the cup-shape indusium of the sori; **G.** An approximate view of the alternate inserted apical round to reniform sori. A–E and G, exhibit photos from the leaves 21 to 24, from the herbarium of the *Muséum National d'Histoire Naturelle* (MNHN), Paris (disposable online in <https://science.mnhn.fr>). The illustration of the sample in F, was taken from the catalogue of the herbarium material of the Royal Botanic Garden of Edinburgh herbarium (number 1537, from <http://data.rbge.org.uk/herb/E00183364>). Scale bars: A, 5 cm; B–D and F, 1 cm; E, 2 cm; G, 5 mm.

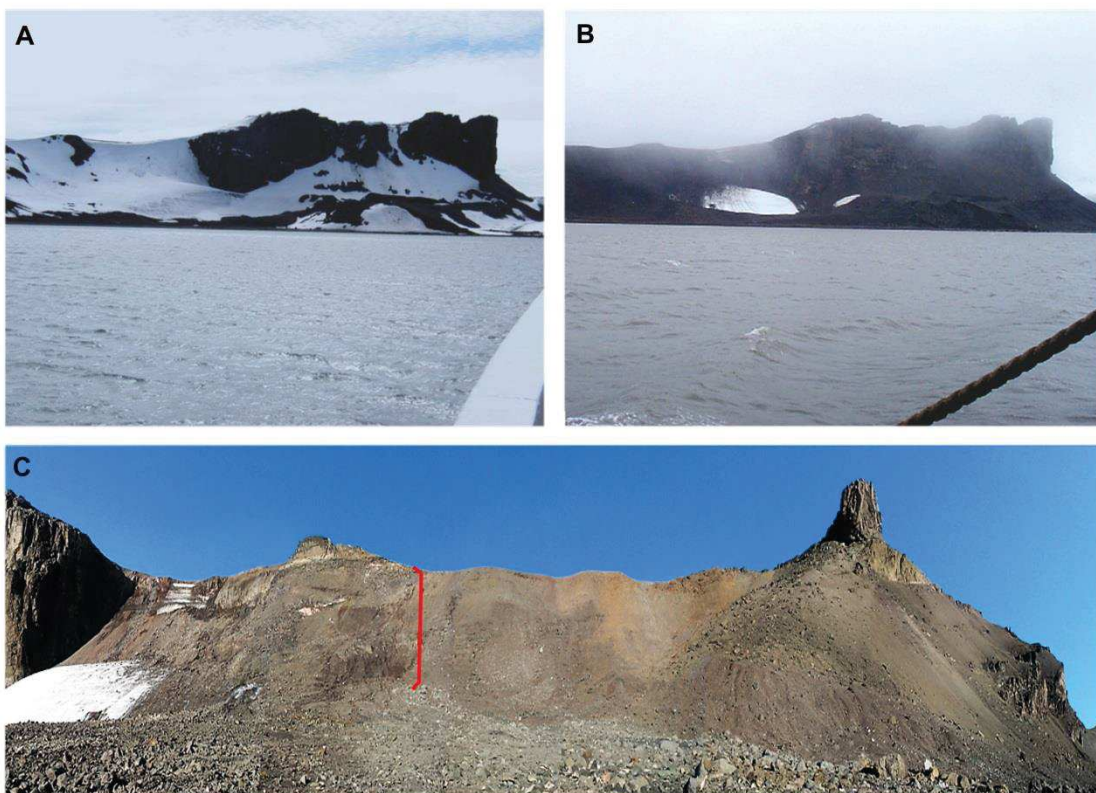


Figure 3. **A.** General view of Hannah Point, seen from the western sector of Walker Bay, in February of 1981 (at left) and 2007 (at right); **B.** Next view of Hanna Point in a

sunny day and the location of fossiliferous beds (red line), detailed in Figure 4. Photos from M. Leppe (INACH).

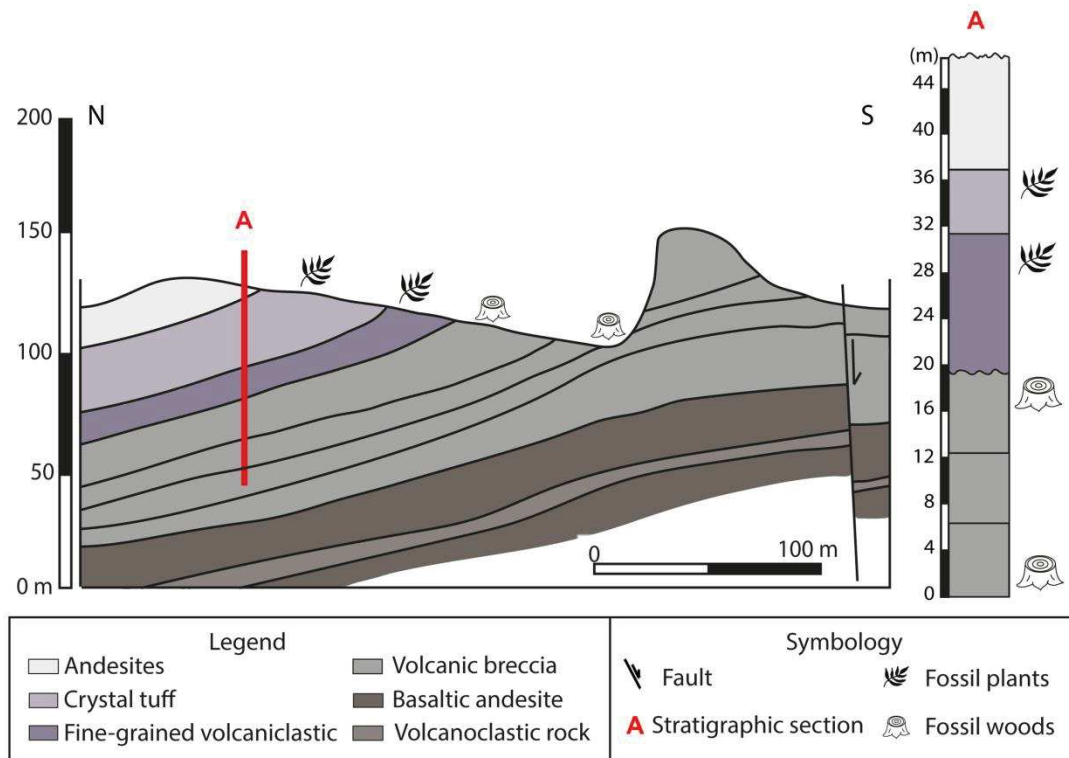


Figure 4. Geological cross-section along the Upper Cretaceous volcanic succession of Unit D from Hanna Point deposits (modified from Pallàs et al., 1999), and the plant beds location. The red line A indicates the sector of the vertical profile at right.

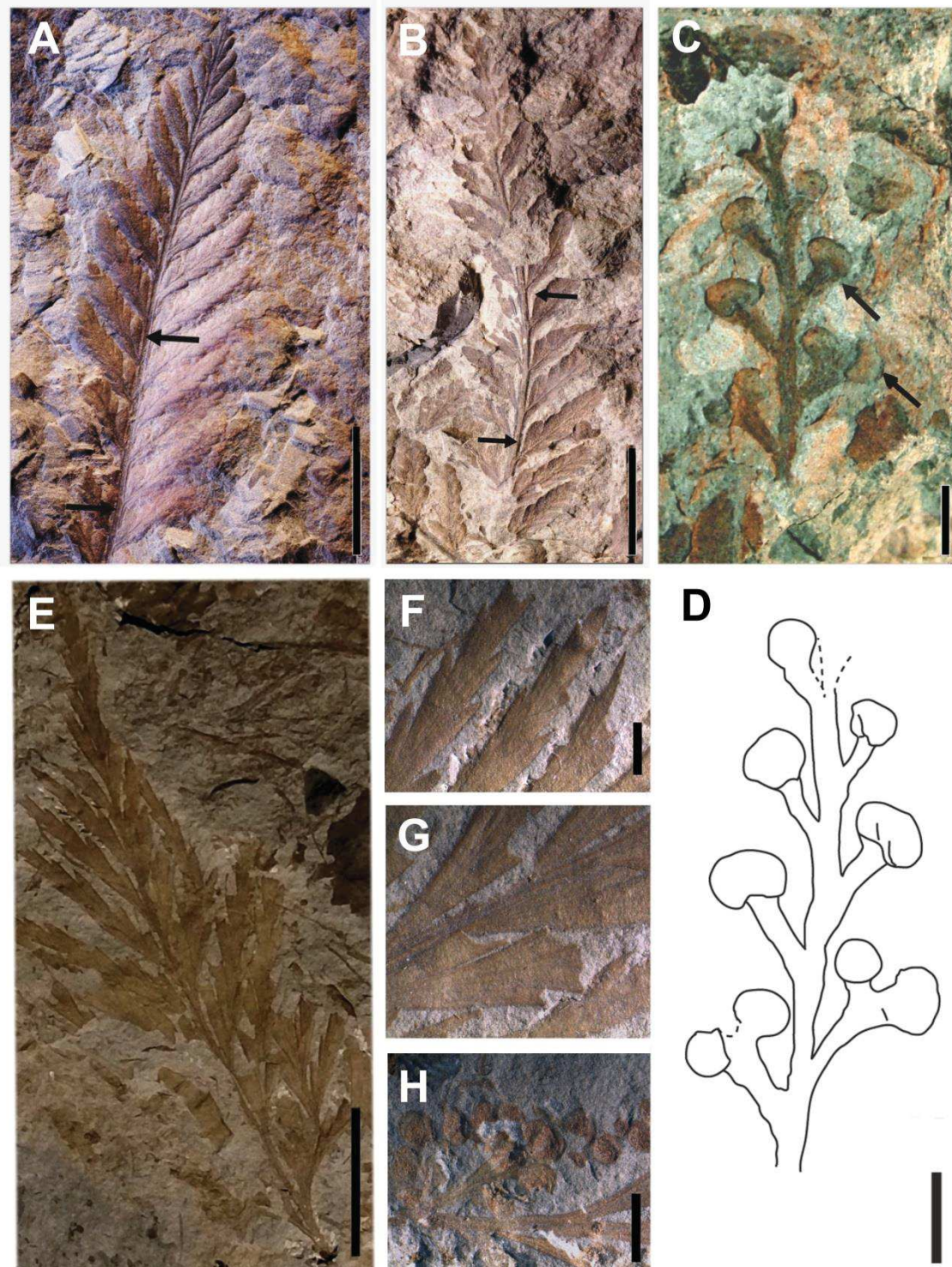


Figure 5. Holotype of *Thyrsopteris elegantiforma* nov. sp. (CPAP 2408 - INACH). **A-B.** The cast of the adaxial side of a more basal sterile pinna highlights the grooved rachis (low arrow in A) and the alternate asymmetric and acroscopic pinnules, of the decurrent base and lobate margins. The upper arrow point to the characteristic well-developed basal pinnule lobe, parallel oriented in relation to the rachis; **C-D.** The

impression of probable terminal pinnae with more dissected pinnules of decurrent bases (arrows); **E-F**. Fertile pinnule with slender stalks of reduced laminas, carrying reniform to round sorus of cyathiform indusium (upper arrow in E), inserted over a clavate receptacle. The low arrow points to the bifurcated basal stalks. Scale bars: A–B, 1 cm; C, 5 mm; D, 2 mm; E-F: 5 cm

| TAXA | kind of remain | Age | Stratigraphic unit | Outcrops | Place | References |
|---|-------------------|-----------------------|---|-------------------------------------|----------------|---|
| <i>Coniopteris</i> sp. B 5622B ¹ <i>C. hymenophylloides</i> Harris ¹ | Fertile pinnae | Mid-Upper Jurassic | Mount Flora Fm. | Hope Bay, Graham Land | Antarctic Pen. | <i>Gee (1989); Rees and Cleal, 2004 (Pl. 8-2). Age: Birkenmayer and Ociepa (08)</i> |
| <i>Cyathidites minor</i> Couper | spore | Jurassic.-K | Ferrar/Bacon Group | Victoria Land | E Antarctica | <i>Couper, 1953; Norris, 1965</i> |
| <i>Cyathidites minor</i> , <i>C. australis</i> +< | spore | Tithon.-Berrias. | Locality 1 | Byers Peninsula | Antarct. Pen. | Askin, 1981, 1983 |
| <i>Cyathidites</i> spp. ³ | spore | Berriasian | Eromanga/Surat | Many localities | E-W Austra. | <i>Dettman et al., 1992</i> |
| <i>Cyathidites minor</i> | spore | Berrias-Albian ? | HawksCrag Breccia | Fox River, Nelson Is. | N. Zealand | <i>Couper, 1953; Norris, 1968</i> |
| <i>Cyathidites australis</i> Couper | spore | Berrias-Albian ? | HawksCrag Breccia | Ohika Beds | N. Zealand | <i>Norris, 1968</i> |
| <i>Onychiopsis psilotoides</i> ⁴ | dimorphic | Early K. | Nyker Group. | Bornholm | Denmark | <i>Friis and Pedersen, 1990</i> |
| <i>Cyathidites minor</i> , <i>C. australis</i> , <i>C. aspera</i> Dettman ⁵ + | spore | Valang./Haut.. | Flora D, Byers Gr. | Presid. Head, Snow Isl. | Antarct. Pen | <i>Philippe et al 1995; Torres et al., 1997</i> |
| <i>Cyathidites minor</i> ; <i>C. australis</i> ; <i>C. concavus</i> Dettmann | spore | Berrias.-Valang. | Chester Cone Fm. President Beaches F | Presid. Head, Snow Isl. | Antarct. Pen. | <i>Hernandez and Azcarate, 1971; Duane, 1996</i> |
| <i>Cyathidites</i> spp. + | spore | Aptian | Byers Group | Presid.Head, Snow Isl. | Antarct. Pen. | <i>Poole & Cantrill, 2006</i> |
| <i>Cyathea cyathifolia</i> nov. sp. | pinnae | Aptian | Baqueró Group | Austral Basin | Argentina | Villar de Seoane, 1999 |
| <i>Cyathidites minor</i> | spore | Aptian | Ohyka beds | Fox River, Nelson Is. | N. Zealand | Couper, 1953 |
| <i>Cyathidites</i> sp. (~ <i>T. elegans</i>) + | spore | Aptian | Ohyka beds | Fox River, Nelson Is. | N. Zealand | Couper, 1953 |
| <i>Cyathidites minor</i> | spore | Aptian | Baqueró Group | Patagonia | Argentina | Vera, 2010 |
| <i>C. patagonicus</i> + | spore | Aptian | Baqueró Group | Patagonia | Argentina | Vill. de Seoane, 1999; Vera, 10 |
| <i>Cyathidites minor</i> ⁸ + | spore | Aptian-Albian | Walker Bay erratics | Walker Bay/Livingston | Antarct. Pen | Chen et al., 2015 |
| cf. <i>C. concavus</i> , <i>C. australis</i> | spore | Aptian-Albian | Walker Bay erratics | Walker Bay/Livingston | Antarct. Pen | Chen et al., 2015 |
| <i>Cyathidites</i> Couper + | spore | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | <i>Césari et al., 2001; Césari, 2006</i> |
| <i>Cyathidites australis</i> Couper + | spore | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | <i>Hathway et al. 99; Vera, 2010</i> |
| <i>Kuylisporites</i> sp. | spore | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | Vera, 2010 |
| aff. <i>Cyathea tyrmensis</i> Krassilov | perm stem | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | <i>Césari et al., 2001</i> Age data: <i>Hathway et al., 1999</i> |
| <i>Cyathidites</i> sp. | spore | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | <i>Césari et al., 2001</i> |
| <i>Thyrsopterorachis mesozoica</i> Nish.& Nishida | perm stem | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | <i>Césari et al., 2001</i> |
| <i>Eocyathea remesaliae</i> Césari (ex- <i>C. tyrmensis</i> Kras.) | frond/spore | Aptian-Camp. | Cerro Negro Fm. | Byers Pen./Livingston Rotch Dome | Antarct. Pen. | <i>Césari, 2006</i> Age data: <i>Parica et al., 2007</i> |
| aff. <i>Cyatheaceae</i> | perm. stem | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | Vera, 2010; <i>Philippe et al. 93</i> |
| aff. <i>Cyatheaceae</i> | perm. stem | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | <i>F.-Lang & Cantrill, 2002; Vera, 2010</i> |
| <i>Rafaherbstia nishidai</i> nov. sp. ⁹ | perm. stem | Aptian | Cerro Negro Fm. | Byers Pen./Livingston | Antarct. Pen. | Vera & Césari 2018 |
| <i>Yavanna chimaerica</i> Vera ⁶ #* | perm. | Aptian | Cerro Negro Fm. | Rotch Dome, Byers Pen., | Antarct. Pen. | Vera, 2013 |

| | | | | | | |
|--|-----------------|---------------|------------------------|--------------------------|----------------|--|
| (~ <i>Lophosoria quadripinata</i>) | stem/spore | | | Livingston | | |
| <i>Cyathidites minor</i> | spore | Aptian | Cerro Negro Fm. | Byers Pen., Livingston | Antarct. Pen. | Hathway, 1999 |
| <i>Cyatheales</i> indet. | stem | Aptian | Cerro Negro Fm. | Rotch Dome, Livingst. | Antarct. Pen. | Vera, 2010, 2015 |
| <i>Alienopteris livingstonensis</i> Vera #* | perm. stem | Aptian | Cerro Negro Fm. | Byers Pen., Livingst. | Antarct. Pen. | Vera, 2009 |
| <i>Cyathidites minor</i> , <i>C. australis</i> + | spore | Albian | Type A flora | Cape Shirreff, Livings. | Antarct. Pen. | Palma-Heldt et al. 2004, 2007 (age: Haase et al. (2012)) |
| <i>Cladophlebis dissecta</i> Nagalingun & Cantrill ^{2a} . | sterile pinnule | Albian | Triton Point Fm. | Alexander Island | Antarctic Pen. | Nagalingun and Cantrill (2015, Fig. 5A, 5C and 8E) |
| <i>Natalipteris wildei</i> Vera & Herb. ^{7#} | stem | Albian-Turon. | Mzinene Fm. | Swaziland | S. Africa | Vera & Herbst, 2015 |
| <i>Kwazulupteris schaarschmidtii</i> ^{7*} | stem# | Albian/Turon. | Mzinene Fm. | Swaziland | S. Africa | Vera & Herbst, 2015 |
| <i>Coniopteris distans</i> Orlando | pinna | Cenomanian | tuffaceous boulder | Williams Pt./Livingston | Antarct. Pen | Orlando 1968; Lacey y Lucas 1981 |
| <i>Coniopteris</i> sp. | | | | | | |
| <i>Thyrsopterorhachis mesozoica</i> | stem | Cenom.-Maast | remobilized | Hokaido | Japan | Nishida & Nishida 1979 |
| <i>Heilongjiangcaulis keshanensis</i> ⁷ | stem # | Cenom.-Maast | Quantou-Mingshui | Songliao Basin | NE China | Cheng & Yang, 2017 |
| <i>Cyathidites</i> sp. and other ferns + | spore | Cenom.Camp. | interbedded with tuffs | SW Williams/ Livingst. | Antarct. Pen | Chapman & Smellie, 1992 |
| <i>Cyathidites minor</i> | spore | Santon.-Camp. | moraine erratics | Hanna Point./ Livingst. | Antarct. Pen. | Palma-Heldt et al. 2004, 2007 |
| <i>Thyrsopteris</i> sp. | pinnae | Santon-Camp. | - | Hanna Point./ Livingst. | Antarct.Pen. | Trevisan <i>et al.</i> , 2015 |
| <i>Cyathidites</i> sp. | spore | Camp-Maast.? | - | Rip Point, Nelson Isl. | Antarct.Pen. | Dutra <i>et al.</i> , 1996 |
| <i>Thyrsopteris</i> sp. | pinna | Camp-Maast. | - | Cerro Guido | South Chile | Kunze, 1834 |
| <i>Thyrsopteris</i> sp. | pinna | Camp-Maast. | - | Cerro Guido | South Chile | Hooker, 1846; Trevisan <i>et al.</i> , 2016 |
| <i>Asplenium dicksonianum</i> Kurtz | pinna | Camp-Maast. | Dorotea Fm. | Cerro Guido | South Chile | Kurtz, 1889; Hünicken, 1971 |
| <i>Thyrsopteris antiqua</i> Menéndez * | fertile pinn | Camp-Maast. | Dorotea Fm. | Cerro Guido | South Chile | Menéndez, 1966, 1972 |
| cf. <i>Thyrsopteris elegans</i> Kunze | sterile pin. | Camp-Maast. | Half Three Pt. Fm. | Skua Bay, Fildes, KGI | Antarct.Pen. | Dutra & Batten, 2000; Dutra <i>et al.</i> , 2014 |
| <i>Cyathidites minor</i> | spore | Camp.-Maast? | Rip Point | N of Nelson Isl. | Antarct.Pen. | Trevisan <i>et al.</i> , 2011 |
| <i>Cyathidites minor</i> | spore | Camp.-Maast. | Half Three Pt. Fm. | Fildes, KGI | Antarct.Pen. | Cao Liu, 1990, 1994 |
| <i>Cyathidites</i> cf. <i>C. minor</i> | spore | Camp.-Maast | Half Three Pt. Fm. | Fildes Pen., KGI | Antarct.Pen. | Cao Liu, 1990, 1994 |
| <i>Cyathidites pulchellus</i> Cao | spore | Camp.-Maast | Half Three Point | Half Three Point, KGI | Antarct.Pen. | Cao Liu, 1994 |
| <i>Cyathidites</i> sp. | spore | Camp.-Maast | Half Three Point | Price Point, Fildes KGI | Antarct.Pen. | Trevisan, 2011 |
| <i>Cyathidites minor/C. australis</i> | spore | basal Maast. | Snow Hill Isl..Fm. | James Ross Isl. | Antarct.Pen. | Di Pasquo & Martin, 2013 |
| <i>Cyathidites minor/cf. C. australis</i> | spore | K-Pg. | L.de Bertodano Fm. | Seymour Isl. | Antarct.Pen. | Bowman et al., 2014 |
| cf. <i>Thyrsopteris elegans</i> | pinnules | Paleoc./Eoc. | Fossil Hill | Fildes, KGI | Antarct.Pen. | Torres, 1990 |
| <i>Thyrsopteris shenii</i> Zhou et Li ⁰ | pinnae./spore | Paleoc./Eoc. | Fossil Hill Fm. | Fossil Hill, Fildes, KGI | Antarct.Pen. | Zhou & Li, 1994a (Plate 2) |
| <i>Cyathidites minor</i> , <i>C. australis</i> , <i>C. patagonicus archangelsky</i> | spore | Paleoc./Eoc. | Fossil Hill Fm. | Fossil Hill, Fildes, KGI | Antarct.Pen. | Torres & Méon, 1990; Cao Liu, 1994; |
| <i>Cyathidites minor</i> | spore | Eocene | Fossil Hill Fm. | Norma, Fildes, KGI | Antarct.Pen. | Torres & Méon, 1990 |
| <i>Alsophila antactica</i> Christ * | pinnae # | Paleoc./Eoc. | Fossil Hill Fm. | Fossil Hill, Fildes KGI | Antarct.Pen. | Zhou & Li, 1994a |

| | | | | | | |
|---|--------------|--------------|-------------------|--------------------------|--------------|---|
| <i>Asplenium antarcticum</i> Dusén * (~ <i>T. shenni</i>) | pinnae | Paleoc./Eoc. | Fossil Hill Fm. | Fossil Hill, Fildes, KGI | Antarct.Pen. | Czajkowski & Rössler, 1986, Tab. IV and V |
| <i>Cyathoides thyrsopteroide</i> Berry ^{2b} | sterile pin. | Paleoc.-Eoc | Concep.- Arauco | Curamilahue | Chile | Berry, 1922. |
| <i>Pteridophyta (Cyatheaceae?)</i> * | pinnules | Paleocene | Sobral Fom. | Seymour Island | Antarct.Pen. | Case, 88 (figs. 3B,3C) |
| <i>Thyrsopteris shenii</i> Zhou et Li ¹ | pinna./spore | Eocene | Fossil Hill Fm. | Rocky Bay,Fildes,KGI. | Antarct.Pen. | Zhou & Li, 1994a |
| <i>Pteridophyta (~Thyrsopteris)</i> * | pinnules | Eocene | Point Henn. Group | Admiralty Bay, KGI | Antarct.Pen. | Zastawniak, 1981 (pl. 1, fig.3) |
| <i>Cyathidites minor</i> + | spore | Eoc./Olig. | Chenque/Cullen Fm | San Julian, San Jorge | Fuego Land | Zamaloa, 1999 |
| <i>Dicksonia patagonica</i> Berry ^{2c} ? | pinnae | Mid-Eocene | Rio Pichileufú | Rio Negro | Argentina | Berry 1938. Age of Wilf et al., 2005 |
| <i>Dendropteridium cyatheoides</i> | stem | Neogene | volcanic rocks | Mount Elgon | East Afr. | Bancroft, 1932 |

Table 1. The record of Cyatheaceae and *Thyrsopteris* related forms in deposits surrounding the Pacific, Indian and southeastern oceans ordered by age. Some other tree ferns sharing *Thyrsopteris* features (e.g. *Coniopteris* and *Onychiopsis*) are also included. Botanical affinities after Askin (1990); Césari (2006); Raine et al. (2011); Bowman et al. (2014); Nagalingum and Cantrill (2015).

Symbols: Asterisks (*) dubious related species or revised in its taxonomic assignment; (+) main component of the fern assemblage; (#) species assigned to “core tree ferns” *sensu* Bystriakova et al. (2011); (<) associate acritarchs indicates near coast deposits. Abbreviation: KGI= King George Island

Obs:

¹ fertile pinnae similar to that of *Thyrsopteris* by the fine slender stalk bearing transversally orientated sori and the apparent cup shape indusium;

- ^{2a} sterile and fertile fronds similar to *Thyrsopteris*. Differs, however, by the whole base attached pinnules and the catadromic secondary veins, with ramifies in both sides of the main vein (Nagalingum and Cantrill, 2015, Figs. 5A, 5C and 8E)
- ^{2b} sterile frond similar to that in *Thyrsopteris* and with *Dicksonia patagonica* Berry, 1938
- ^{2c} sterile and fertile fronds very similar to that of *Thyrsopteris* in the gross morphology (see text),
- ³ *Cyathidites* spore grain could represents both Cyatheaceae and Dicksoniaceae (Nagalingum et al. 2002). To Raine et al. (2011), between other options, refers to *Thyrsopteris*.
- ⁴ Considered similar to *Thyrsopteris* by the alternate arranged, stalked fertile units. Included in Dicksoniaceae by Friis and Pedersen (1990);
- ⁵ Considered in Osmundaceae (Torres *et al.*, 1997).
- ⁶ show similarities with both *Thyrsopteris elegans* Kunze and Cyatheaceae s.s., suggesting represents an extinct lineage of Cyatheales (Vera, 2013; Cheng and Yang, 2017)
- ⁷ may be referred to as ‘core tree ferns’ or an ancestral form of Cyatheaceae (Cheng and Yang, 2017); to Vera and Césari (2018), the last option is more probable.
- ⁸ pteridophytes are 86% of the assemblage and attest a regularly perturbed riparian setting in which episodic volcanism (Chen et al., 2015);
- ⁹ at moment considered a a non-cyatheaceous taxon (Vera and Césari, 2018).

Comprovante de submissão do artigo II

Successfully received: submission Ferns from the Late Cretaceous bed..

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Ferns from the Late Cretaceous beds of Cerro Guido (Tres Pasos Formation), Magallanes Basin, Chilean Patagonia

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Abstract

The Late Cretaceous succession of Cerro Guido, in the Magallanes-Austral Basin of Southernmost Chile, is part of one of the most important known high paleolatitude fossil assemblage, by containing continental floras and vertebrate remains associate to marine faunas. With the beginning of the Gondwana break-up and the consequent changes in the global climate and palaeogeography, these plants grew during a period of global greenhouse climates, in near-coast deltaic or estuarine areas. The herein analysed pteridophytes are for the first time described and were identify in levels of the de dominant marine deposits of the Campanian Tres Pasos Formation. In the macroflora, ferns are a subsidiary component in an angiosperm-conifer and *Taeniopteris*, probably surrounding vegetation. The results show terrestrial ferns, of an understorey vegetation composed by dominant *Cladophlebis* (Osmundaceae) and *Alamatus*, associates with forms related to extant *Alsophila* (Cyatheaceae) and *Anogramma* (Pteridaceae). Some of them are common in other Southern Hemisphere floras; meanwhile others are until now exclusive of the Campanian and Maastrichtian floras of Antarctic Peninsula. The Tres Pasos assemblage is related to near coast deposits, and by the evidence of the remobilizing of its remains, probably grows around the body waters linked to intertributary rivers.

Key words: Pteridophytes, Campanian, Cerro Guido, Magallanes basin, Tres Pasos Formation.

1. Introduction

The early Late Cretaceous is considered an interval when the globe was characterized by warm climates (Huber et al., 1995; Gallagher et al., 2008), attested by high atmospheric CO₂ (Wang et al., 2014; Linnert et al., 2014) as well as warm sea surface temperatures (Miller et al., 2005). However, by the end of Campanian to the early Maastrichtian (ca. 71 Ma) a continuous fall in the global temperature is recorded (Barrera and Savin, 1999; Francis and Poole, 2002; Bowman et al., 2014) and coincides with strong changes in the vegetation structure. At this time, the angiosperms begin to dominate the forests and increase in diversity and dominance (Wing and Boucher, 1998), thanks to its rapid reaction in response to changing environments. It will alter fundamental aspects of global and ecosystem ecology, shifting the trajectory of many lineages evolution (Beerling and Osborne, 2002).

At the same time, Cretaceous marks the explosive rise of modern groups of leptosporangiate ferns (Schneider et al., 2004; Schuettpelez and Pryer, 2009), that also pass by radiations and evolutive events, like the widespread appearing of epiphytic species (Watkins and Cardelús, 2012). Nowadays, ferns are distributed in almost all environments, where are often restricted by the climate and altitude (Kessler et al., 2001). They demonstrate a high capacity of adaptation at disturbed environments and, by its broad fossil record, they can provide important ecological and paleoclimatic informations (Collinson, 2002). By extinction of some forms of the stem group and by the conviviality between relicts of them and those representing the new adaptations, the Cretaceous and the immediate times of the K-T boundary could had been critical to the history of the pteridophytes, mainly for the ones who grew up in those high latitudes (Schuettpelez and Pryer, 2009)

The fossil ferns herein studied were preserved on levels of Campanian to Paleogene age, exposed at the Cerro Guido, in Chilean Patagonia (Fig. 1). They attest a flora still not quite understood and described, despite their worldwide-recognized importance, since the 19th century (Hauthal, 1898, Kurtz, 1899, Florin, 1940; Feruglio, 1949-50; Cecioni, 1957; Yabe et al., 2006). Known by 'Flora of Kurtz', its paleobotanical record is recognized by their diversified content and by testimony the arrival of the flowering plants in conifers and other gymnosperms forests, and pteridophytes. The first collection of the fossil flora was studied by Hauthal (1898) and was after sent to Kurtz, who made the first approach to its taxonomy. Afterwards, Berry (1937) and Hünicken (1971) revised the plant fossil collection, criticizing the Kurtz affinities made with floras from the North Hemisphere.

Leppe et al. (2012) compare the Cerro Guido Flora along with other austral assemblages looking by the establishment of its current distribution. In its proposal, continuous forests existed in southern South America and Antarctica, and had been shaped along the Upper Cretaceous, by the presence of marine basins and intermittent connection and disconnection of the landmasses.

All of these previous works are in accord about the scarce presence of the pteridophytes on Cerro Guido. Meanwhile, recent paleontological campaigns have allowed the identification of new plant beds in Tres Pasos Formation, in fine sandy intercalations at the lower and middle part of the southern flank of Cerro Guido (Figs. 2). The main goal of the present study is to identify this new fossil fern material and contribute to the paleogeographic and paleoenvironmental reconstructions of this southernmost pit of South America at the end of Cretaceous.

2. Geological setting

The Late Cretaceous strata of the Province of Ultima Esperanza was part of the Magallanes- Austral basin deposits, a north-south foreland basin developed along the Andes fold-thrust belt system (Macellari et al., 1989; Fildani et al., 2009; Romans et al., 2010, 2011), and that accompany the N-S current territorial boundary of Chile and Argentina. Many authors studied the stratigraphic sequence of the Magallanes Basin (Hauthal, 1907; Quensel, 1911; Cecioni, 1957; Katz, 1963; Cortés, 1964; Macellari, 1988; Schwartz et al., 2016). The resulting proposals highlight their general condition of a retro-arc foreland basin, preserved in the Andean fold-and-thrust belt and formed in an extensional phase associated with the initial break-up of the Gondwana (Upper Jurassic). Those tectonic efforts originate the oceanic backarc basin of Rocas Verdes, that precedes the Andean uplift (Wilson, 1991; Fildani et al., 2003, 2008; Katz, 1963; Schwartz et al., 2016).

The deep-water sedimentation on the basin started with the onset of the foreland basin in the Turonian and persisted for >25 million years, coinciding with the Punta Barrosa, Cerro Toro (Turonian-Campanian) and Tres Pasos (Santonian-Campanian) formations deposition, which ages informed by detrital zircon U-Pb analysis (Romans et al., 2010; Bernhardt, 2011; Schwartz et al., 2016). The diversified depositional settings and deposits include unconfined-basin-floor sandstones, coarse-grained channel-complex-fill and mud rich mass-transport deposits (slumps, slides, and debris flows). This deep-water cycle will be covered in the end of Campanian to Maastrichtian, by the shallow marine to deltaic sediments of Dorotea Formation (Katz, 1963; Macellari et al., 1989; Fildani et al., 2007; Romans et al., 2011; Schwartz and Graham, 2015; Gutiérrez et al., 2017, see also Fig. 3). In the neighbourhood locality of El Puesto, vertebrates bones of Hadrosaurs, Mosasaurs and Plesiosaurs were identified in upper levels of Tres Pasos Formation (Vogt et al., 2014), also characterized by the presence of plant fossils,

insects, and abundant traces of *Skolithos* and *Thalassinoides* (Covault et al., 2009; Hubbard et al., 2010). Part of the Tres Pasos succession is represented by shallow marine deposits (shoreface or foreshore), attesting the presence of storm episodes, with accumulation of coquina layers and calcareous concretions containing abundant shell fragments. There the presence of *Panopea* sp. and *Pterotrignia windhauseniana* confirm the Late Cretaceous age (Vogt et al., 2014). Other facies inform about subaerial and overbank floodplains with small channels and shallow ponds, crevasse splay structures and partially filling interdistributary bays, containing fossil wood, leaves and pollen grains (Gutiérrez et al. 2017). However, to Schwartz et al. (2016) those deposits represent delta fronts, tidal influenced upper deltas and lower delta plains with interdistributary channels.

Those deposits are concordantly overlaid by the basal part of Dorotea Formation (Fig.3), and attest to the gradational transition between deep to shallow marine contexts (Schwartz et al., 2016). For Katz (1963) and Macellari (1988), conglomerate lenses and marine fossils (bivalves, gastropods and ammonites) are also present. Fining-upward conglomerates fill the channels and contain fossil woods and leaf fragments, bivalves, shark teeth and oyster accumulations, had been assigned to estuarine or interdistributary bays environments.

The fern pinnae and pinnules herein described (Fig. 4), was found associated to coal lenses and originate from levels of the Tres Pasos Formation and by its fragmentary preservation, allows inferring that a previous remobilization of plant remains occurred. They were obtained from two basal levels of the southern flank of Cerro Guido (CG2-8F and CG2-7F;), respectively composed by sandstones to sandy mudstones of yellowish grey colours, and mudstones. The location of the plant fossil beds between two levels containing the ammonite *Hoplitoplacenticeras plasticus*

Paulcke, provides a good support to the Santonian-Campanian proposed age of Tres Pasos Formation, recently confirmed by analysis of detrital zircon U-Pb (Gutiérrez et al., 2017).

By attesting the sea levels changes occurred at the end of Cretaceous and Early Paleogene, with intercalate marine and continental deposits of rich fossiliferous content, the Magallanes-Austral basin were ever focused on deep attention. The successions have only similar comparative in the well-known and coetaneous deposits of James Ross Basin, in northeastern Antarctic Peninsula, aligned between the most extensive known back arc deposits (Reguero et al., 2003). During great part of the Late Cretaceous continuous lands still link the Eastern flank of the Antarctic Peninsula and Patagonia, only interrupted during short intervals of sea level rising and greenhouse conditions (Miller et al, 2003) and the initial efforts of Gondwana breakup between Southern America and Antarctic Peninsula, at the end of Cretaceous (Elliot, 1988; Smith and Anderson, 2010)

3. Material and methods

The analyzed material (80 samples) was collected in the expeditions of the Chilean Antarctic Institute (INACH, Punta Arenas, Chile), on summer seasons of 2012 and 2016, in an exposition of the volcanic-sedimentary rocks of Magallanes Basin at Cerro Guido (Fig. 3). The fossil flora, especially those related with the pteridophytes, are preserved by impressions of sterile pinnae and pinnules (level CG2-7F), some covered by iron oxides (level CG2-8F). They occur associated to other plant groups, represented by isolate leaves of *Taeniopteris* Brongniart (Gymnosperm *insert sedis*), few conifers (*Podocarpus inopinatus*, Florin), and distinct groups of arbustive angiosperms (Malvaceae and Myrtaceae). A total number of 20 samples refer to

pteridophytes remains, lodged within the Paleontological Collection of Antarctic and Patagonia from INACH (Chilean Antarctic Institute), at Punta Arenas, Chile, under the museum acronyms CPAP 4890 to CPAP 4910. Despite its partial preservation and the unfavourable sand size grains, fine details were preserved.

An Olympus SZH10 stereo microscope with a drawing attached device was used on the analysis of morphological appeals after recorded with a Canon DSLR EOS digital camera using both polarised light and filters to enhance contrast, or low-angle lighting to reveal surface detail. Fine features were drawing over the photos using Adobe Illustrator CC. On the describing and comparisons of morphological features, previously described fossils from the Antarctic Peninsula and South America were analyzed. The taxonomic insertion was based in the proposals of Korall et al. (2006), Smith et al. (2006), and Cristenhusz and Chase (2014). An analysis looking for associated spore grains shows unfertile materials. However, due to the fragmentary state of the material, represented only by sterile and partially preserved pinnae, a dubious affinity with the previously known species and genus are maintained.

4. Systematic Paleontology

Division Pteridophyta

Class Polypodiopsida

Order Osmundales

Family Osmundaceae Berchtold and J. Presl.

Cladophlebis Brongniart emend. Frenguelli 1947

Type species: *Cladophlebis albertsii* (Dunker) Brongniart 1849

Cladophlebis sp.

(Fig. 4A-B)

Materials: CPAP 4893, the impression of a pinna fragment and pinnules, covered by iron oxides, which highlight the vein pattern (level CG28F)

Description: incomplete sterile pinna of sessile pinnules, of least 20 mm long and 10 mm wide. Pinna rachis stout and straight, 1 mm wide. Lanceolate oblong pinnules, alternate inserted in the rachis at 40-45° angles, with slight crenulated margins and with obtuse to the subacute apex. Midvein prominent, wide in basal part, thinning upward and sometimes bifurcating, not reaching the apex. Catadromic lateral veins, alternate dispose and closely spaced, bifurcate one or two times nearly above the midvein.

Remarks: The isolated pinna fragment herein described differs from most of the other previously forms linked to *Cladophlebis* genus by the absence of falcate pinnules and by its entire (or weakly lobate) margins. Some similarities were detected on the general pinnules form and its catadromic veins, e.g. with *C. denticulata* (Brongniart) Fontaine and *C. antarctica* Nathorst (in Halle, 1913), both described to the Jurassic and Early Cretaceous of Antarctica (Gee, 1989; Rees and Cleal, 2004; Nagalingum and Cantrill, 2015). However, by the entire margins, considered a key character to Gee (1989, pg. 166) and Rees and Cleal (2004, pg. 25), *Cladophlebis* sp. from Cerro Guido differs from those two species and until the finding of new materials remains uncertain in its specific affinity.

aff. *Cladophlebis oblonga* (Halle) emend. Rees and Cleal

(Fig. 4C-D)

Materials: CPAP 4894, the cast of a part of pinna and pinnules covered by iron oxides (level CG28F)

Description: Sterile pinna fragment with also a straight rachis (1 mm wide), bearing sessile oblong pinnules (2 cm long in average) with a slight constrict base, alternate inserted at broad angles (60° to 80°), entire margin, acute apex and prominent base. The straight midvein presents a slight decurrent course ending in the apex. Lateral veins once time dichotomized, soon after the midvein.

Remarks: The specimen here described is here assign to aff. *C. oblonga* by its pinnules shape, obtuse apex and the numerous lateral veins typically once forked, characteristic of the species described by Halle (1913). By those appeals and taking in account the unique sample disposable, is only possible suggests an affinity with *C. oblonga*, a species found in Jurassic levels of Hope Bay, Antarctic Peninsula (Gee, 1989; Rees and Cleal, 2004), only differing by the presence of falcate pinnules on the Graham Land materials. The Early Cretaceous *C. oblonga*, identified in Alexander Island by Nagalingum and Cantrill (2015), shows similar pinnules of the broad angle of divergence and entire margins, but sharply differs by the mucronate apex and opposite pinnules insertion.

aff. *Cladophlebis auriculipilosus* Mays and Tosolini

(Fig. 4E–F)

Materials: CPAP 4895, part of pinna and pinnules preserved by casts (level CG27F).

Description: Sterile pinna fragment with straight rachis (5 mm of wide). Sessile pinnules (15 mm long, 7 mm wide), sub-opposite inserted at angles between 86° to 97° , oblong in shape, with entire margins and exhibiting a small round auricle in the acroscopic side. Apices broadly obtuse. The presence of an auriculate base gives a kind

of asymmetry to the pinnules and influence the main vein to assume a more basiscopic course. Lateral veins dichotomize one or two times, far from the costa.

Remarks: The specimen here described is morphologically nearly identical to *C. auriculipilosus* Mays & Tosolini, from the Late Cretaceous of New Zealand (Mays et al, 2015), by the presence of the characteristic auricle and hastate pinnules with asymmetric midvein. More specific affinities are here prevented by the incomplete preservation.

Observations about the *Cladophlebis* related forms: the pinnule morphology of the forms herein described fits well with those considered by Brongniart (1849) when treating of this genus, e.g., sessile pinnules, straight rachis, most falcate pinnules with pectopteroid venation. On recent works, such kind of sterile foliage, despite being considered of difficult taxonomic insertion, had been included in the Osmundales (Vakhrameev, 1991, Tidwell and Ash, 1994; Escapa and Cúneo, 2012). However Seward (1894), without the preservation of fertile material or the anomocytic stomata, a kind of uncertainty is maintained about its relation at the order level. Still on, *Cladophlebis* might also represent the sterile foliage of some other fern families, e.g., Cyatheaceae, Schizaeaceae, and Dennstaedtiaceae (Villar de Seoane, 1996) due to its highly homoplastic character (Escapa and Cúneo, 2012). A formal survey by other *Cladophlebis* representatives in the Western Gondwana austral areas during Jurassic and Cretaceous was not made due to its abundance in nearly all know basins.

Order Polipodiales

Family Pteridaceae E.D.M. Kirchn

Genus Anogramma Link 1841

Type species: *Anogramma leptophylla* (L.) Link 1841

aff. *Anogramma leptophylla*

(Fig. 4G–J)

Material: CPAP 4896, CPAP 4897, with a delicate pinna and pinnules covered by iron oxides, preserved as impressions in carbonate rocks (level CG27F).

Description: Sterile pinnae fragment with adaxially grooved rachis (0.5 mm wide). The trilobed (symmetric) fan-shaped pinnules (10 mm large, 12 mm wide) are also lobed and regularly spaced, with narrow bases and rounded apices. Veins free, the main one diluting and forked once to twice. Lateral veins of catadromic course.

Remarks: In the comparisons made with the fossil record, similar forms are absent, meanwhile, the extant *Anogramma lepidophylla* shows many common features with the Cerro Guido pinnae (Duncan and Isaac, 1986). Both have fan-shaped trilobed pinnules with opposite lobes and narrower bases. The presence of *Anogramma* indicates shallow soils, similar to that today found in the forests of the coastal areas of Tasmania and Victoria, in Australia, and in New Zealand, South America, India, Africa and Europe (Duncan and Isaac, 1986)

In the leaflets, also *Asplenium dareoides* share an affinity, although it differs by the asymmetric character and coriaceous texture.

Order Cyatheaales

Family Cyatheaceae Kaulf.

Alsophila R. Brown. 1810

(Fig. 4K–L)

Materials: CPAP 4897, a cast of fragmented pinna and pinnules covered by iron oxides (level CG28F).

Description: a coriaceous sterile pinna, bearing oblong-lanceolate pinnules, forming narrower angles in relation to the rachis (10-25°), with sessile broad bases, crenate margin and acute or mucronate pinnule apex. In the pinnules, the forked secondary veins (near the costa) normally has two lateral branches. Together with the other features above commented, it distinguishes *Alsophila* from *Chyatea*.

Remarks: The modern *Alsophila* compound a clade extends into the southern temperate zones and at some sub-Antarctic areas (Auckland Island), where are found in the cloud or wet montane forests, where characterize the medium-understorey. With a main distribution in the Pacific coast of most South Hemisphere areas (including South Africa), they also can colonize the open or disturbed lands (Tryon and Tryon, 1982; Large and Braggins, 2004; Marquez and Ponce, 2011). In Antarctic Peninsula, *Alsophila antarctica* Christ ex Dúsen was previously described by Dúsen (1908) to the Paleocene-Eocene levels of Seymour Island and assigned it to *Dicksonia antarctica* (ex-), after also identified in the Lower Eocene levels of Fildes Peninsula, in King George Island (Zhou Zian and Li Haomin, 1994). However, most of the remains are restrict to sterile fronds and of *Alsophilidites* Cookson spore grains, which was also identified in Campanian levels of the Half Three Point Island of the same King George Island (Dutra and Batten, 2000). Today *Alsophila* accompany the other cyatheaceous tree ferns in its pantropical distribution.

The supposed first record of the Cyatheaceae foliages is surrounded by some controversial interpretations about its original location in North or Southern Hemisphere. The form of the Jurassic of Poland (*Alsophilites polonica* (Hirmer) Raciborsky), was after reconsidered by Chu Chia-Nan (1963), when describing *Cyathea ordosica* Chu, from levels of the same age from Inner Mongolia. What seems to be a more secure record of a cyatheaceous fern is the permineralized stems of the primitive

Oguracaulis, from Tasmania (Tidwell and Ash, 1994; Collinson, 1996), by its anatomic features, that lead Copeland (1947) proposes that the origin of the tree ferns occurs in the Jurassic of Antarctica, a proposal after supported by Tidwell and Ash (1994). Sterile and fertile foliage assigned to *Cyathea*, identified in the Early Cretaceous of Patagonia, was described by Villar de Seoane (1999), that points to the conservative characters of its habitat and of morphological and anatomic appeals.

Family uncertain sedis

Alamatus Douglas 1973

Type species: *Alamatus biffarius* Douglas

aff. *Alamatus biffarius* Douglas

(Fig. 4M-N)

Material: CPAP 4898, with an impression of ultimate branches of the sterile pinnae, with many filiform secondary pinnae and without a preserved stipe (level CG27F).

Description: sterile deeply dissected pinna dichotomizing in three steps, each one containing at least seven (in the preserved form) pinnules (apical ones 3,5 cm long and 3 mm wide). The pinnules, acutely inserted in the pinna (angles of 10°–12°), has entire margins, acuminate to truncate apices, characterized by only one vein.

Remarks: Similar structures and morphologies were found in pinnae from the Early Cretaceous of southern Australia, where they had been assigned to three distinct genera (*Aculea*, *Alamatus* and *Amanda*) by Douglas (1973), based in the position of the sori. Between them, the form herein described shows a preferable affinity with *Alamatus* Douglas, by the presence of the distinct grades of pinnae. Forms of the genus also recorded in Cenomanian levels of the Eromanga Basin, in Australia (McLoughlin et al., 1995). *Alamatus* and *Aculea* are also recorded in Albian levels of Alexander Island,

Antarctic Peninsula (Cantrill, 1996). *Aculea* share common pinna features but have fewer segments of a more symmetric and organized disposition.

Similar deeply dissected, bi- to trifurcate fronds with filiform pinnules, also characterizes the Pteridaceae *Actiniopteris* Link (Duncan and Isaac 1986), today growing in mountainous regions of tropical and subtropical regions of the Old World within African-Asian area of distribution (Vaganov and Shmakov, 2016). By the filiform pinnules and its dichotomization, the here described pinnae also resemble the fronds of modern Schizaeaceae, as for example, some species of *Schizaea* genus, e.g. *S. dichotoma* (L.) Sm. and *S. asperula* Wakefield.

5. Final Remarks

The presence of a preserved flora on levels of the Tres Pasos Formation, despite its poor diversity and fragmentary state, is unexpected when considering that in the paleoenvironmental reconstructions, its deposition was considered had been occurring in a continental-margin slope systems (Shultz et al. 2005; Fildani et al., 2007; Hubbard et al., 2010). Meanwhile, could be in accord with their fragmentary character and the presence of isolate ultimate pinnae, which suggest their previous remobilization. Their allochthonous preservation is in agreement with the high dynamic conditions that involved the near coast environments inferred to the Tres Pasos Formation, yet difficult its apply in the paleoenvironmental reconstructions.

Considering this, the proposal of a shoaling upward succession seems to be more parsimonious, mainly if its association with coal lenses are considered. Deposited near areas under the tectonic influence, the Tres Pasos and Dorotea formations succession confirm the gradual transition from a near slope deposits to a shore face and deltaic context (Covault et al. 2009), the last stage been confirmed by the levels characterized

by plant fossils. Along with conifers and angiosperms remains, the fern flora informs about a vegetation that probably grows in the coastal areas, where ferns communities probably inhabited the understory of vegetated areas surrounding the floodplains, marshes and deltas (Vakhrameev, 1991; Wang, 2002; Van Konijnenburg-van Cittert, 2002). This is the case when we see the modern affinities of *Alsophila*, some Osmundaceae and of *Anogramma leptophylla* (Escapa and Cúneo, 2012; Gonzatti et al., 2016), and those inferred to the fossil genus *Cladophlebis* (Barbacka and Bodor, 2008; Escapa and Cúneo, 2012) and *Alamatus* (Douglas, 1973; Cantrill, 1996)). All those forms, and the conjunct occurrence with alloctonous mollusc shells confirm that transitional near coast environments controls part of the deposition of Cerro Guido.

Additionally, is important to highlight that despite the fossil remains can reach the coastal areas, the presence of the scaly tree ferns, indicates that surround or next highlands, conformed by volcanic processes and covered by cloud forests exists (Kramer, 1990).

6. Conclusion

The Upper Cretaceous (Campanian) deposits of the Tres Pasos Formation, in Cerro Guido, with a diversified assemblage, yet represented by few fragmentary specimens, provide important elements to inform about the establishment of terrestrial ecosystems, after a long time of sea influenced deposits in the retroforeland Magallanes-Austral basin. The fern community herein described is still interesting by its coincidence with a time of expressive evolutive and ecological changes, marked by the angiosperms irradiation and the diversifying of the pteridophytes crow group. It fits also with a global warm episode, with high atmospheric CO₂ concentration and extensive changes in geography and climate due to the Gondwana breakup, which creates

favourable conditions to plant radiation on the high southern latitudes. The fossil assemblage of Tres Pasos Formation, by join typical Mesozoic ferns forms, like *Cladophlebis* and *Alamatus*, mixed to core fern groups, some still alive (*Alsophila*), contributes also to confirming the end-Cretaceous age proposed by the radiometric data.

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Figure and captions

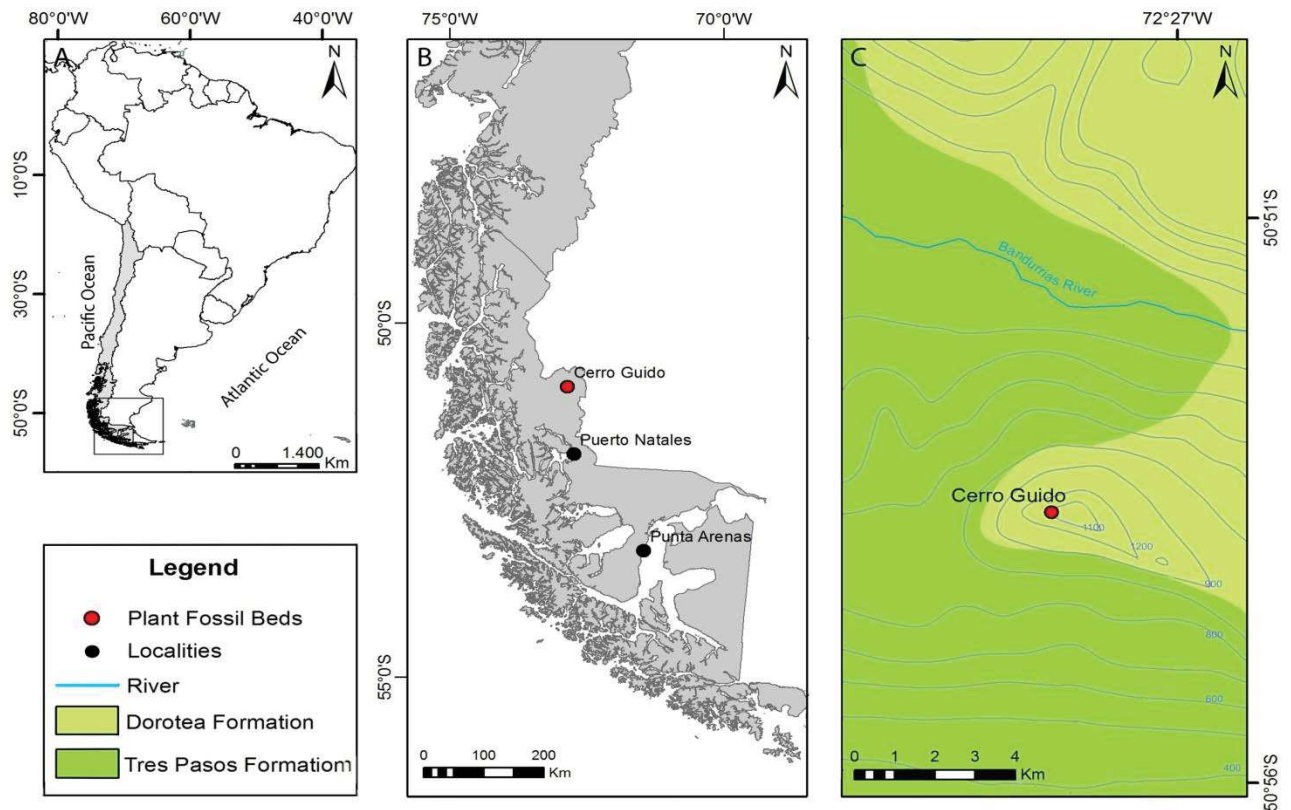


Figure 1. A. General map of South America highlighting the Chilean Patagonia; B. Cerro Guido location in Ultima Esperanza Province, Chilean Patagonia; C. Areal distribution of Magallanes-Austral Basin stratigraphic units (Tres Passos and Dorotea formations) in the region of Cerro Guido.



Figure 2. General view of Cerro Guido and the approximate location of the transitional boundary between Tres Pasos and Dorotea formations (white line). Photo from C.T.

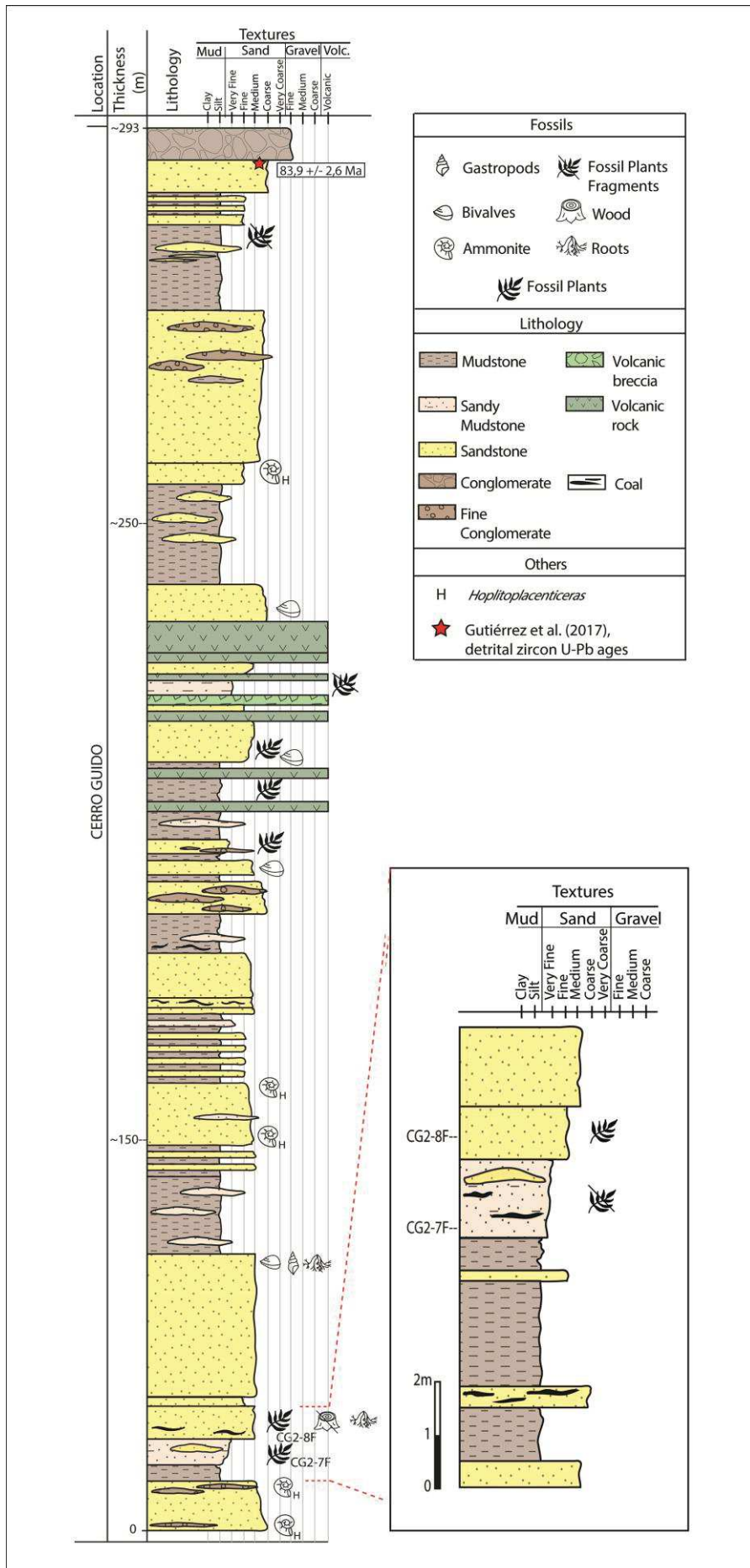


Figure 3. Stratigraphic profile of the Cerro Guido and the levels that probable marks the transition between Tres Pasos and Dorotea Formations (the black arrow and coinciding with the last occurrence of *Hoplitoplacenticeras*) and the location of plant fossils levels (CG2-7F and CG28F).

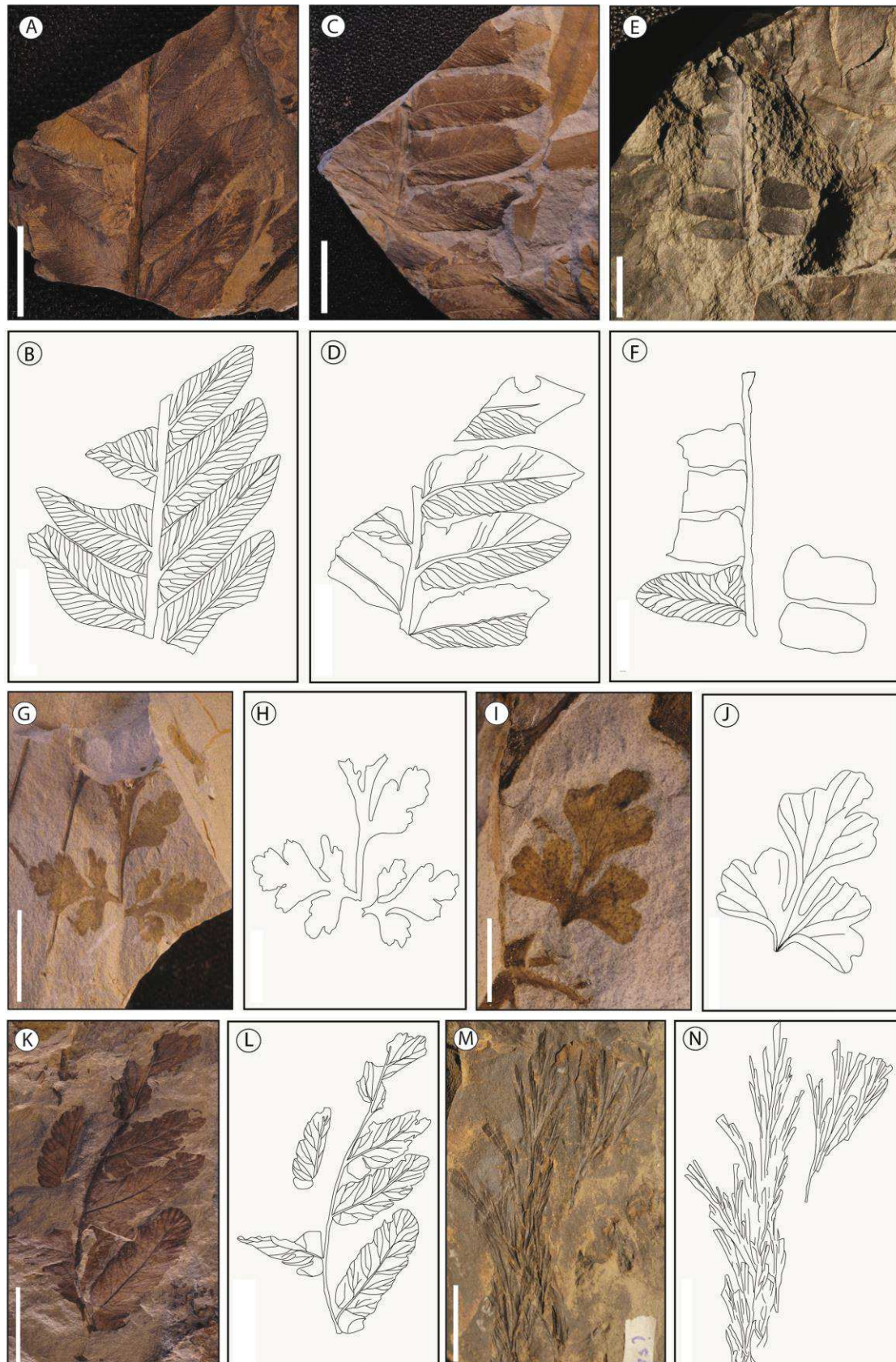


Figure 4. Pteridophytes of the Tres Pasos Formation in basal-mid levels of Cerro Guido, Chile.
A-B. *Cladophlebis* sp.; **C-D.** *Cladophlebis* aff. *C. oblonga*; **E-F.** *Cladophlebis* aff. *C.*

auriculipilosus; **G-H-I-J.** *Anogramma* aff. *A. leptophylla*; **K-L.** *Alsophila* sp.; **M-N.** *Alamatus* aff. *A. bifarius*. Scale bars = 1 cm.

4. Síntese Integradora

A posição estratégica ocupada pela Península Antártica e Patagônia nos últimos 100 milhões de anos torna o estudo de seus fósseis, especialmente aqueles representados por restos de plantas, importantes para compreender a origem das modernas floras do Hemisfério Sul e sobre seu comportamento diante das variações climáticas globais e da geografia. A diversidade de ambientes criados pelos eventos tectônicos nas áreas austrais do Gondwana e as condições amenas e úmidas do clima no extremo final do Cretáceo, parece ter sido a principal causa para significativas mudanças na fisionomia da vegetação. As pteridófitas constituíram um componente importante nas floras fósseis das áreas da Península Antártica e da Patagônia no final do Cretáceo e presenciaram a chegada das angiospermas às altas latitudes, permitindo o surgimento de novos componentes comparáveis aos grupos modernos. O aprofundamento dos estudos deste grupo de plantas para estas áreas, aqui apresentado, contribui na reconstrução dos biomas austrais e colabora nas implicações evolutivas e paleoambientais ocorridas para o final do Cretáceo. Os resultados alcançados permitiram atestar a ocorrência da mais antiga forma do gênero *Thyrsopteris* e a descrição de formas inéditas para os depósitos de Cerro Guido, no Sul do Chile, apoiando a hipótese de que as altas latitudes exerceram forte influência na origem de muitos grupos de pteridófitas.

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