PALEOGENE IMBRICATE-LEAVED PODOCARPS FROM KING GEORGE ISLAND (ANTARCTICA): ASSESSING THE GEOLOGICAL CONTEXT AND BOTANICAL AFFINITIES

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ABSTRACT – Imbricate-leaved podocarps (*Dacrydium* s.l.) are the dominant conifer remains in the Upper Cretaceous and Cenozoic successions of King George Island, increasing its abundance in the post-Late Paleocene strata and maintained until the Early Oligocene times, with poor taphoflora registered in the last. However, a more precise taxonomic relationship of their remains was ever difficult given the fragmentary nature of the fossils and most known from *ex situ* material. In new field works and collections looking for the original levels, the recent phylogenetic approaches proposed and comparisons with extant floras have been applied to these fossils, and have helped to clarify their taxonomic status and their preferable association with the Upper Paleocene-Lower Eocene levels. The two kinds of foliage discussed here initiated the taxonomic revision of the Podocarpaceae related fossils on the island and attest to a modern affinity with *Dacrydium* vel *Halocarpus* and *Dacrycarpus*, which was in part proposed by previous works. Those genera comprise today an important component of the eastern Southern Hemisphere forests, and their occurrence in the Antarctic Peninsula areas during the Paleogene supports a broader distribution in the past and attests to the importance of the ancient Antarctic coastal areas in the modern distribution of the Podocarpaceae.

Key words: *Dacrydium* s.l.*, Dacrycarpus,* Lower Eocene, King George Island, Antarctic Peninsula.

RESUMO – As Podocarpaceae são o principal grupo de coníferas nas floras do Cretáceo-Paleógeno da ilha King George, Península Antártica e, após o final do Paleoceno, tipos dotados de folhas pequenas e imbricadas, inicialmente agrupados em *Dacrydium* s.l., passam a ser dominantes nas assembléias. O caráter incompleto dos fósseis, que dificulta uma atribuição taxonômica mais precisa, fez também com que este epíteto genérico, sem afinidades filogenéticas bem estabelecidas, fosse muito utilizado nos primeiros estudos feitos. Novas análises e a ampliação das coletas, embora não tenham solucionado de todo este problema, mostraram ser úteis para tornar mais precisos os tipos de Podocarpaceae presentes. Neste trabalho, dois morfotipos são revistos e sugerida sua afinidade preferencial com *Dacrydium* vel *Halocarpus* e *Dacrycarpus*, hoje importantes componentes dos biomas do setor oriental do Hemisfério Sul. São igualmente localizados de modo mais preciso e a partir de novos trabalhos de campo, os níveis com plantas do Monte Wawel (= Pontal Hennequin), na baía do Almirantado, previamente conhecidos a partir de material *ex situ,* o que permitiu propor uma idade Eoceno Inferior para estes depósitos. A presença destes gêneros de Podocarpaceae em áreas da Península Antártica durante o Cenofítico, não apenas confirma sua ocorrência mais ampla no passado, como o importante papel exercido pelas áreas costeiras da Antártica na moderna distribuição da família.

Palavras-chave: *Dacrydium* s.l., *Dacrycarpus*, Eoceno Inferior, ilha King George, Península Antártica.

INTRODUCTION

A great diversity of fossil plants has been collected from King George Island (KGI), South Shetland Islands, Antarctic Peninsula (Figure 1). Many of the taxa found are coniferous and include the Araucariaceae and Cupressaceae, but by far, the most abundant are those with affinities to the Podocarpaceae (Birkenmajer & Zastawniak, 1989; Zhang Shanzen & Wang Qingzhi, 1994; Zhou Zhian & Li Haomin, 1994a).

Podocarpaceous foliage compressions and impressions have also been found in fossil assemblages across the Southern Hemisphere, since their first remains were discovered in the 19th century. They have often been assigned to two broad and informal taxa based on the arrangement and size of the leaves, *Podocarpus* s.l. and *Dacrydium* s.l. (Philippi, 1861; Florin, 1931; de Laubenfels, 1969). This taxonomic treatment was still applied to extant groups until the 1980s and sometimes used in the determination of the scarce and incomplete plant fossil material, such as those found in most of the KGI fossil assemblages (Zastawniak, 1981; Zastawniak *et al.*, 1985).

The identification of new fossil material in Australia and New Zealand, some associated with reproductive structures and cuticles (Wells & Hill, 1989; Hill & Carpenter, 1991; Pole, 1992; Jordan, 1995; Hill & Christophel, 2001), allows advances

in the taxonomic placement of podocarpaceous fossils (Hill & Brodribb, 2003), also with the help of the re-evaluations in taxonomy and phylogeny of extant Podocarpaceae (Quinn, 1982; Chaw *et al.*, 2000; Kelch, 1998). A long geological history for the Podocarpaceae and a monophyletic origin emerges from those works, in common with that from the Taxodiaceae and Cephalotaxaceae, and with a close relation with the Araucariaceae.

The Podocarpaceae probably originated at the end of the Paleozoic, and by the Triassic they are evidenced by *Rissikia* and *Mataia* from Chile, Australia, New Zealand and South Africa (Townrow, 1967; Anderson *et al.*, 2007; Herbst *et al.*, 2005), and in the pollen assemblages (*Podocarpidites* and *Dacrycarpites*) from the northwestern Argentina area (Zavattieri, 1990). In the uppermost Triassic, cuticles with a podocarpoid character were found associated with conifer shoots in southern Brazil (Dutra & Wilberger, 2010). The Triassic shoots (*Rissikianthus*), cones (*Rissikistrobus)* and wood (*Notophytum krauseli*) identified in the Fremouw Formation also confirms Antarctica as an important location in the family's first appearances (Meyer-Berthaud & Taylor, 1991; Axsmith *et al.*, 1998).

The Podocarpaceae maintained a dominant austral distribution throughout the Jurassic and at the beginning of the Cretaceous, and advanced into more tropical latitudes, taking advantage of the equable warm climatic conditions and the continuous landmass of Pangaea (Pearson *et al.*, 2001), to finally reach the Northern Hemisphere (Mill, 2003; Fontes, 2008). During the Cretaceous, the first modern related forms appeared in the South America-Antarctic region, both in macroassemblages and pollen grains (Halle, 1913; Romero & Arguijo, 1981; Askin, 1990; Cao Liu, 1992; Zhou Zhian & Li Haomin, 1994b; Dutra & Batten, 2000; Francis *et al.*, 2008).

During the Cenozoic, the group maintained its southern high latitude distribution, mainly during the warm intervals of the Paleocene-Eocene Thermal Maximum (PETM) and Early Eocene Climatic Optimum (EECO), between 55 and 52 Ma (Zachos *et al.*, 2003; Shellito *et al.*, 2003). The worldwide distribution is preserved until the beginning of the Neogene, when Antarctic isolation and CO_2 decrease resulted in a global climatic cooling and restriction of high latitude biomes (Zachos *et al.*, 2001; Francis *et al.*, 2008). The Podocarpaceae seemed less affected by these low temperatures than other austral conifers and were thus able to persist for a relatively long period in high latitudes, including the South Pole area (Francis & Hill, 1996). According to Pole (2001) and Winkworth *et al.* (2002), the diversity shown by the podocarps during the Late Cenozoic and today in New Zealand results from secondary radiations, and long distance dispersal occurred at specific times during their geological history.

Today, the family represents the largest and most diversified group of conifers, growing mainly in altitudinal mesic forests, either mixed with angiosperms or in nearly pure stands (Quinn & Price, 2003). In colder latitudes down to coastal areas, such as on South Island of New Zealand, they experienced oceanic climates (Eckenwalder, 2009). Podocarps with scale-like leaves on the mature shoots can also endure extreme cold, forming pure stands in localities of periodically frozen soils, where could adopt dwarf habits, such the New Zealand and Tasmanian *Halocarpus bidwillii* (Hook *ex* Kirk) Quinn and *Microcachrys* Hooker fil., and the South American *Lepidothamnus fonkii* Philippi (Veblen *et al.*, 1995; Wells & Hill, 1989; Echkenwalder, 2009). The characters proffered by diversified adaptations, with varied shoot morphologies, attest to the plasticity of their foliage. The ability of the Podocarpaceae for long-distance dispersal probably guaranteed long-term survival and wide distribution during geological time (Cubitt & Molloy, 1994; Pole, 2001). These ecological and behavioral aspects support the proposal of Brodribb & Hill (2003) that extreme dry conditions are the only limiting factor to the development and spread of the Podocarpaceae.

In this work, Paleogene imbricate-leaved podocarps from King George Island (Antartica), some originating from newly collected *in-situ* specimens and exhibiting two types of leaf shoots are described and rediscussed in relation to their taxonomic and stratigraphic placement.

Podocarpaceous leaf shoots and taxonomic affinities

The Podocarpaceae have perennial and sclerophyllous foliage, a character that increases their preservation potential and makes them a common feature of the fossil record, especially originating from ancient disturbed areas (Falcon-Lang & Cantrill, 2001). The leaves are spirally arranged and generally simple, entire and decurrent, a morphology that helps in a broad selection and to distinguish them from fossils of other southern conifer remains, such as the Cupressaceae, normally exhibiting whorled phyllotaxis with opposite or decussate leaves (Offler, 1984) and the Araucariaceae, where in similar needle-like leaved shoots the presence of a detached midvein is not common. Yet, higher order (intrafamilial) distinction is often difficult using shoot arrangement and size of leaves alone, since many genera can appear similar (*e.g.* opposite leaf insertion can be found in the podocarp of *Microcachrys* and whorled phyllotaxis in some *Podocarpus*; Offler, 1984; Hill, 1998).

However, within the Podocarpaceae, leaf characters have been used to separate two main groups, *Podocarpus* s.l. (Philippi, 1861), with leaf shoots composed of large, open-arranged needle-like leaves, with one central vein and a common false petiole, and *Dacrydium* s.l., characterized by strongly adpressed, short, imbricate and bifacial flattened leaves, especially in the mature shoots (Offler, 1984; Wells & Hill, 1989; Stockey, 1990; Pole, 1992). The first one includes, for example, *Podocarpus* s.s., *Acmopyle* Pilger, *Afrocarpus* Page and *Nageia* Gaertn, the last distinct in maintaining a great number of veins over the leaf, a plesiomorphic character according to Kelch (1998). The determination of *Dacrydium* s.l. foliage, to which the material presented here refers, is more complex due to the heterophillic character of the shoots in some genera, with mature ones bearing short and imbricate leaves associated with spreading linear ones, or young trees with needle-like sharply pointed subfalcate leaves, which may give rise to small scale-like and closely adpresssed leaves in the adult foliage (*e.g. Halocarpus* and *Dacrydium*).

Florin (1931) divided *Dacrydium* s.l. into sections A, B and C based on leaf shoot and cuticle characters. *Dacrydium*

s.s. was retained in section B, whilst *Lepidothamnus* Philippi, *Lagarostrobos* Quinn and *Halocarpus* Quinn were grouped together in section C based mainly on the morphology of reproductive structures (de Laubenfels, 1969; Quinn & Gadek, 1981; Quinn, 1982). Molloy (1995) created a fourth monospecific genus, *Manoao*, by segregating the species *Lagarostrobus colensoi*. Strong support for the work of Quinn (1982) is provided by other independent studies, such as those of leaf epidermal structures, wood anatomy and pollen morphology (Florin, 1931; Patel, 1967; Pocknall, 1981). More recent molecular studies confirm the polyphyletic origin of *Dacrydium* s.l. (Kelch, 1998; Page, 1999; Chaw *et al.*, 2000).

THE KING GEORGE ISLAND GEOLOGICAL SETTING AND KNOWN TAPHOFLORAS

On King George Island (KGI), two areas are renowned for the presence of diversified and abundant Late Cretaceous to Early Neogene plant fossil assemblages: the Fildes Peninsula and Admiralty Bay (Birkenmajer & Zastawniak, 1989; Wang Yinxi & Shen Yanbin, 1994; see Figure 1). The complex geological context of the island is due to a genesis in a fore arc tectonic region, and coupled with ice cover, which has hindered the determination of a more regional stratigraphic framework and correlations between the fossil plant beds (Smellie *et al.*, 1984; Yanbin, 1994; Birkenmajer, 2001; Dutra, 2004).

On Fildes Peninsula, the first and most widely studied plant fossil succession is that exposed at the top of Fossil Hill, or Mount Flora (62°12'25''S / 58°58'13''W). The first stratigraphic description of this locality was by Smellie *et al.* (1984), later detailed by Shen Yanbin (1994). Plant fossil

assemblages from Fossil Hill were first published by Orlando (1964) and Troncoso (1986), and more intensive collections and systematic studies allowed the founding of at least nine distinct sub-localities (Czajkowski & Rösler, 1986; Torres & Méon, 1990; Cao Liu, 1992; Yanbin, 1994; Zhiyan & Haomin, 1994a,b; Shanzen & Qingzhi, 1994; Dutra & Batten, 2000; Hunt & Poole, 2003; Dutra, 2004), each yielding both a micro- and macroflora, and confirming those floras of Fossil Hill as the most diversified and best preserved ones (Figure 2). The assemblage is made up of angiosperms, with rare but large, broad-leaf types of *Nothofagus*, many ferns, and distinct gymnosperms, with a dominant podocarp component, alongside Cupressaceae and Araucariaceae (Fontes, 2008).

An Upper Paleocene or Lower Eocene age was suggested from palynological studies (Cao, 1992) and Rb-Sr radiometric age data of 58 to 52 Ma obtained on the basal andesitic lavas that were recovered by agglomerates and by the volcanoclastic fining-upward succession that contains the plant fossil remains (Li *et al.*, 1989). The beds were included in the basal part of the Fossil Hill Formation by Yanbin (1994), corresponding to Fildes Formation from Smellie *et al.* (1984).

Within the Fossil Hill outcrop the Podocarpaceae are represented by shoot impressions (Zhiyan & Haomin, 1994a; Fontes, 2008) in a succession that also includes levels with probable impressions of *syneresis* cracks and the until now exclusive evidence of a vertebrate life in the island, represented by bird ichnites belonging to the Ratites (Li & Zhen, 1994), which suggests a deposition on shallow lakes and the rework of volcaniclastic grains by drainages. A second locality on Fildes Peninsula, the Collins Glacier locality, also of a Late Paleocene and/or Early Eocene age, yields many
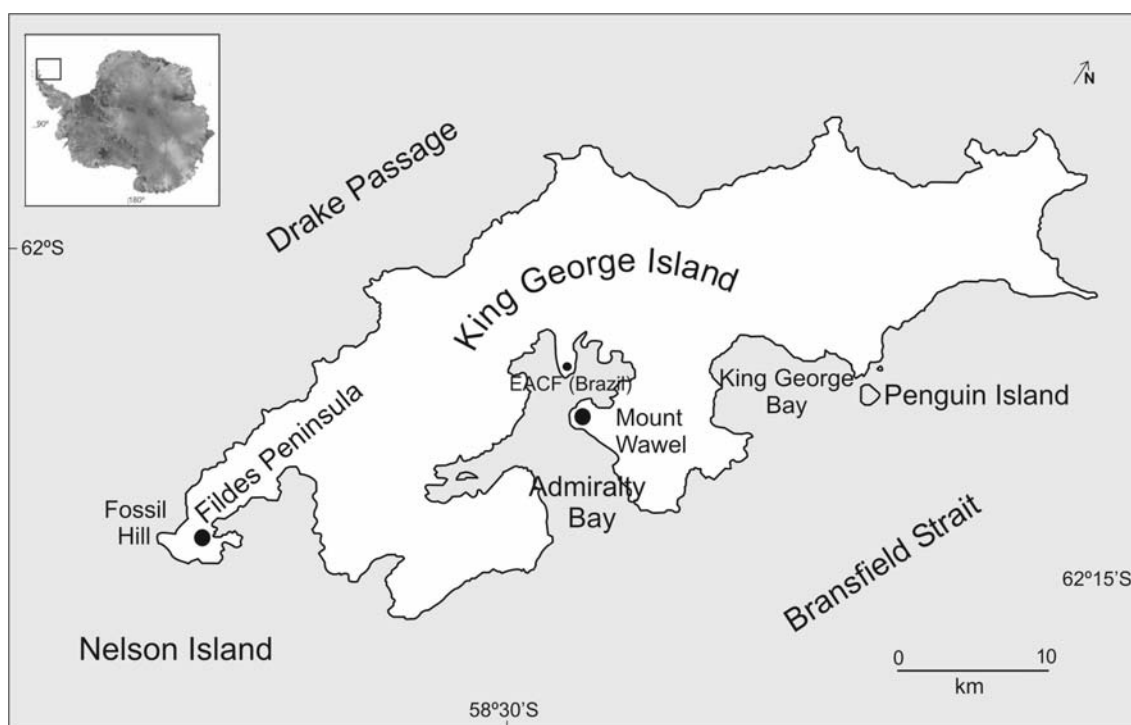

Figure 1. Map of King George Island, showing the main plant fossil localities, Fildes Peninsula and Admiralty Bay. Large dots indicate where podocarpaceous remains have been found.

pieces of fossil wood that include a high podocarp component (Shanzen & Qingzhi, 1994).

In Admiralty Bay, the first geological investigations were undertaken by Hawkes (1961) and Barton (1965), followed by the Polish works coordinated by Birkenmajer, which proposed a more formal stratigraphy for the area (Birkenmajer, 2001). The richest plant fossil assemblage there, and the only one until now, known to preserve podocarp leaf shoots (Zastawniak, 1981; Zastawniak *et al.*, 1985; Poole *et al.*, 2001; Hunt & Poole, 2003), comes from strata along the slopes of the Mount Wawel or Point Hennequin (62°07'00"S/ 58°24'00"W) and was considered to be Lower Miocene in age (Birkenmajer, 2001). The succession, included in the Point Hennequin Group of Hawkes (1961), is exposed at Mount Wawel (Figure 3) and comprises andesitic lava flows (eleven were measured by Barton, 1965), breccias and lapilli, also intercalated by few and thin levels of reworked volcanic material. Birkenmajer (2001) considered that two distinct episodes of tectonic and volcanic activity were preserved in the lava pile, and proposed distinct units, the Vièville Glacier and the Mount Wawel formations, with ages varying, respectively, between 44-47 Ma and 27-24.5 Ma (Pankhurst & Smellie, 1983; Smellie *et al.*, 1984; Birkenmajer *et al.*, 1986).

The fossils are associated with distinct facies on the 300 m high exposure, greatly affected by the faulting and ice covering and reworking. For a long time, this condition prevented the exact understanding of their original location, as they are found in moraine blocks over the low and mid
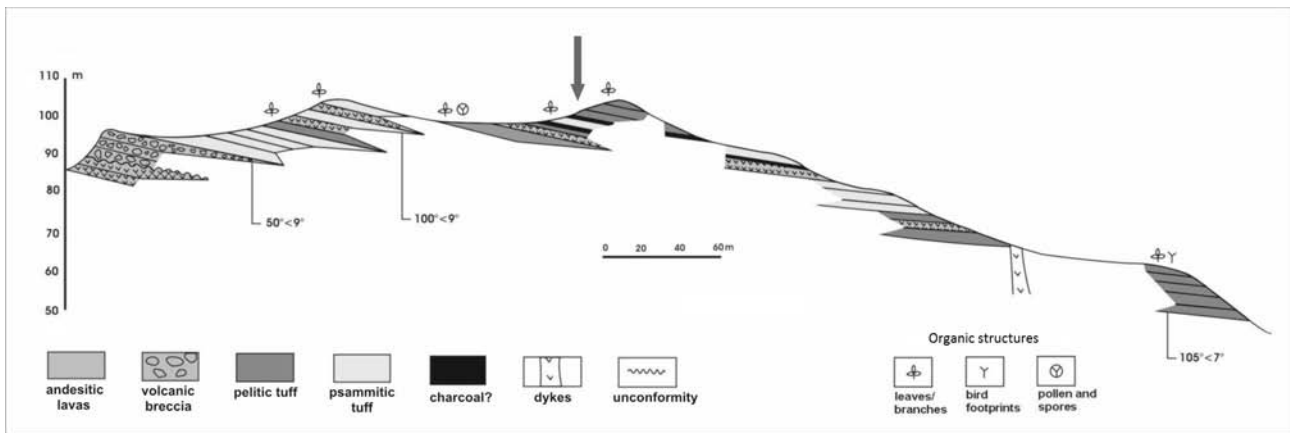

Figure 2. Transection through the top of Fossil Hill (Fossil Hill Formation from Li *et al.*, 1989), on Fildes Peninsula, and the relative positions of the fossiliferous horizons (modified from Yanbin, 1994). The arrow indicates the volcanoclastic beds with concentrated podocarp remains.

Figure 3. General view of the Mount Wawel, Admiralty Bay, with the location of the main fossil plant beds indicated by vertical line on the middle slope. The arrow points to the position of the only known *in-situ* "Mount Wawel plant beds" until 2007 (Zastawniak, 1981; Zastawniak *et al.*, 1985).

slopes of the hill. Only one level at the top of the sequence was considered to be *in-situ* and has been termed the "Mount Wawel plant fossils beds" by Zastawniak (1981). The other *ex-situ* blocks have been referred to as the "Dragon and Wanda Glacier fossil plants beds" and "Smok plant fossil beds" (Birkenmajer, 2001; Hunt & Poole, 2003; Dutra, 2004). According to Zastawniak *et al.* (1985), the origin of the *ex-situ* plant fossil beds was the same from the *in situ* occurrences and designated the beds of the Mount Wawel Formation from Birkenmajer (2001), which guaranteed a Late Oligocene age.

Investigations undertaken across Mount Wawel coupled with an extensive melting of the ice cover in the 2006-2007 summer season, allowed a better establishment of the fossil succession, such that in the mid altitude plants, beds from which part of the *ex-situ* material was originated (Figure 4). Resulting from this, the most basal fossiliferous bed were shown to be the origin of the samples formerly attributed to "Dragon Glacier plant beds" (level A, Figure 4), composed of yellowish, green and brown finely laminated psammitic to pelitic reworked tuffs, deposited in many fining-upward repeating cycles ("varves" of Birkenmajer, 2001). There, the Podocarpaceae represent 56% of the total gymnosperms preserved - a composition similar to that found at Fossil Hill - and influenced the high diversity index (4.7) obtained in the taphoflora. These lower beds are also characterized by the presence of bioturbation, small and thin pavements marked by probable syneresis cracks and raindrop impressions, suggesting ephemeral water bodies, as suggested
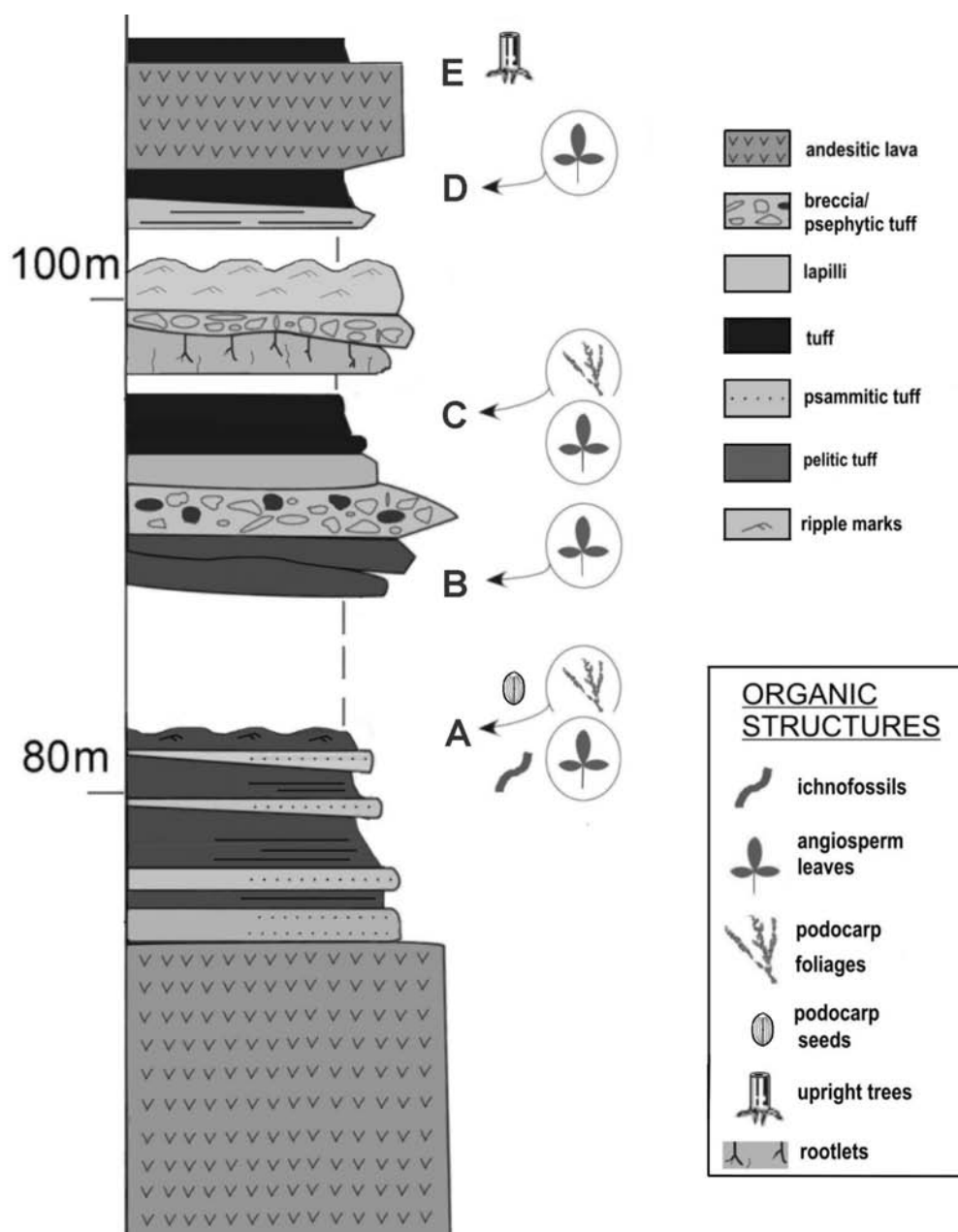

Figure 4. Vertical section from the middle slope of Mount Wawel, with the relative position of the fossil levels described herein. Levels **A**, **B** and **C** correspond to what was called "Dragon Glacier Plant Beds" in previous works; level **D** to the former beds indicate to "Wanda Glacier Plant Beds"; level **E** to that referred to "Smok Plant Beds".

by Birkenmajer (2001). Many small, isolated shoots, leaves and seeds of Podocarpaceae and other gymnosperms (including Araucariaceae), along with fern pinnules and broadleaves of *Nothofagus*, were linked to these levels (Zastawniak, 1981; Fontes, 2008).

Overlying these basal beds and above an unknown interval still covered by ice and moraine material, level B is exposed (Figure 4), composed of dark-brown to grey tuffaceous lapilli, containing poorly preserved angiosperm remains. It is followed by a thick, fining upward succession of dominantly green to yellow and red-green rocks composed of successive levels of agglomerate, lapilli and tuff (level C), and where the upper beds yield a diverse and well-preserved dark-red angiosperm leaves and podocarp shoots. The plant material and lithologies correspond to those described as the "Wanda Glacier plant beds" of Birkenmajer (2001). Within some levels, the plant remains exhibit a unidirectional orientation supporting the idea that they were also laid down in shallow, ephemeral streams (Figure 5). *Ex-situ* beds found at the same altitude allow seeing pavements formed by the reworked volcanic grains and asymmetrical wave ripples (Figure 6). Other pavements exhibit interference ripples with isolated *Nothofagus* leaves with similar genesis, representing the shallow water body supplied by the fluvial streams. Similar depositional structures and preserved plants were

previously identified in this locality by Dutra (2001) and Hunt & Poole (2003) and referred to as "Smok Hill plant beds."

Level D begins with reworked green massive psammites with a conspicuous root horizon (20 to10 cm high) followed by sterile psammitic tuff layer with high-angle cross stratifications, suggestive of surge deposits. This then grades into a cyclic deposition of grey to dark-grey fining upward tuff, representing ash fall deposits (Pereira *et al.*, 2003). Their uppermost layers are covered by isolated and dispersed microphyllic and toothed leaves of *Nothofagus* and Sapindaceae (aff. *Cupania grosse-serrata* Berry), which was also found in the dispersed samples of the "Smok Hill plant bed" by Dutra (2001) and Hunt & Poole (2003). The fossil succession ends with an autochthonous occurrence of charcolified wood located at an altitude of nearly 100 to 120 m (Figure 4, level D).

The discussed fossil content, mainly those from basal levels, marked by a higher floristic diversity, biogenic structures (ichnofossils), and reworked volcanic debris, seems to agree better with those occurring in other sectors of the island, where the ages proposed for the Vièville Glacier Formation (47-44 Ma) seems to be more coherent, than that indicated for the Mount Wawel Formation (27-24 Ma). As a consequence, it prevents at this moment the inclusion of the succession studied, in the formal stratigraphy proposed for Point Hennequin or Mount
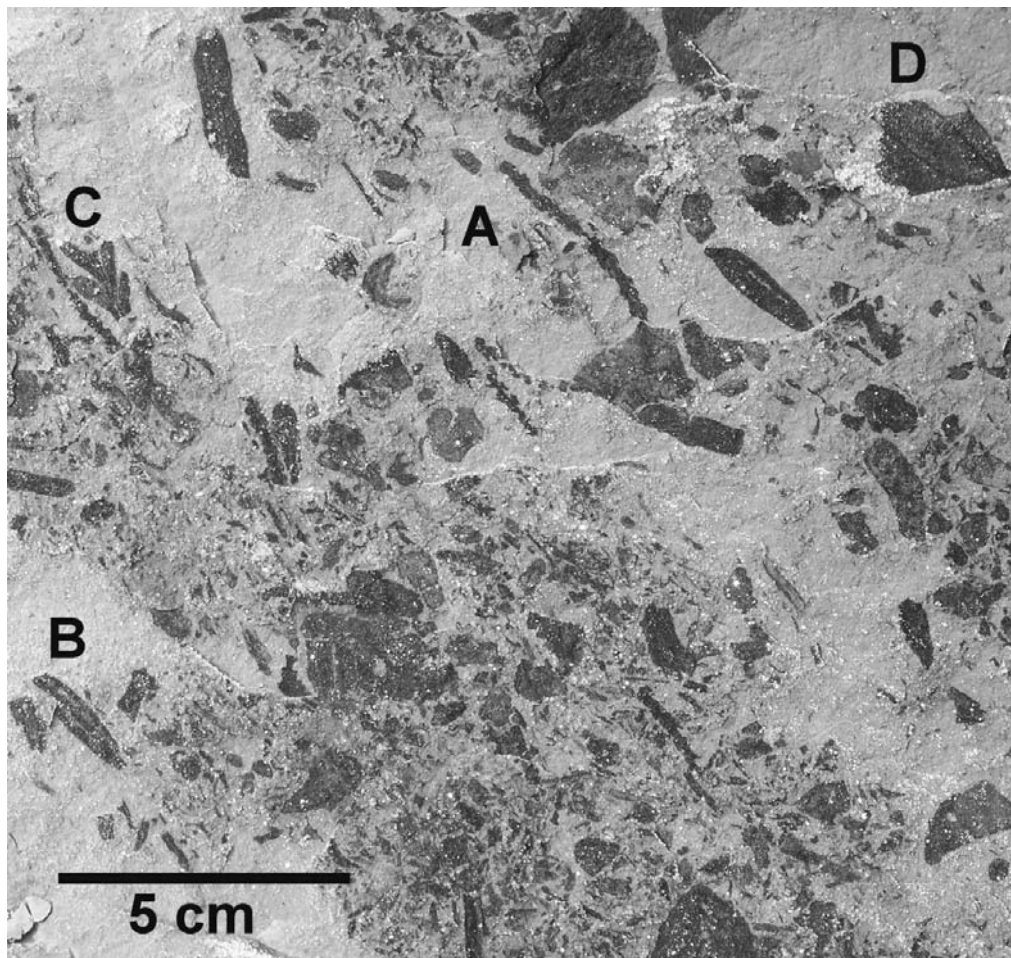

Figure 5. Organic in the Mount Wawel deposits. **A-D**, highly fragmented plant fossil remains, exhibiting a unidirectional orientation, from the more basal beds of level C (see Figure 4), supporting river stream deposition: **A**, scale-like leaf shoots of *Dacrydium* s.l.; **B**, isolated leaves of *Podocarpus* s.l., with its characteristic central vein; **C**, fern pinnules; **D**, parts of *Nothofagus* leaves.

Figure 6. Sedimentary structures in the Mount Wawel deposits. Pavement with asymmetrical wave ripples found on the surface of moraine blocks.

Wawel by Birkenmajer (2001), but it indicates that the older ages determined for the Vièville Glacier are more in line with the information from the fossil content.

Over this, an undetermined part of the profile due to its covering by ice, seems to be formed exclusively by lava beds. The next fossil occurrence corresponds to large seeds of Podocarpaceae described by Zastawniak *et al.* (1985) at the top of Mount Wawel, the "Mount Wawel in situ beds" (Birkenmajer, 2001). The nearly exclusive presence of Podocarpaceae remains at those younger levels provides evidence of the survival of the family in the northern Antarctic Peninsula during the post-Early Oligocene climatic deterioration (Hunt & Poole, 2003; Dutra, 2004; Birkenmajer *et al.*, 2005; Ivany *et al.*, 2006).

In light of the investigations undertaken in 2006-2007, together with previous data from the literature, a tentative correlation with the fossil floras of KGI was proposed (Figure 7). Foremost to making this correlation was (i) the identification of similar processes and fossil assemblages from other Paleogene deposits in the James Ross Basin (Elliot, 1988; Askin, 1990; Cantrill & Poole, 2005), (ii) marker horizons such as those characterized by fossil woods included in lavas and/or agglomerates, that coincides with the upper limit of the most diversified fossil plant successions and preceding those with poorer or no plant assemblages preserved, (iii) the relationship between the main plant beds and the superimposed conglomerate deposits (diamictites/tillites?) registered in some places of the island (*e.g.* upper part of Rocky Bay succession and Point Thomas). In Admiralty Bay,

those deposits were proposed to be linked to an alpine kind of ice covering and with the first evidence of a fall in temperatures, coincident with upper Middle Eocene (Birkenmajer *et al.*, 2005). Similar climate-sensitive deposits and the gradual drop in biotic diversity coincide with the middle part of La Meseta Alloformation on Seymour Island (Gandolfo *et al.*, 1998; Ivany *et al.*, 2008).

MATERIAL AND METHODS

Twenty-four samples containing 50 leaf impression fossils originating from imbricate leaf shoots are discussed here. Additional forms with the same morphology will be the focus of future work. The samples studied here originate from the fossiliferous plant beds of Fossil Hill (Fildes Peninsula) and are designated by the acronym ANTF MF, and *in situ/ex situ* material found on the slopes of Mount Wawel and Szafer (Admiralty Bay) with the acronym ANTF MW and ANTF SZ, respectively. Associated lithologies and charcolified compressions confirm the presence of proximal and active volcanism. With regard to the upper levels of Mount Wawel slopes, as determined by the presence of surge deposits, these volcanic processes had a direct influence on fossil preservation and greatly reduced the chance of leaf cuticle preservation (Pereira *et al.*, 2003). Otherwise, foliage remains are generally preserved as impressions within thin intercalations of reworked volcanoclastic grains deposited in shallow lakes and deltas (Birkenmajer, 2001; Poole *et al.*, 2001; Dutra, 2001, 2004; Figure 4).
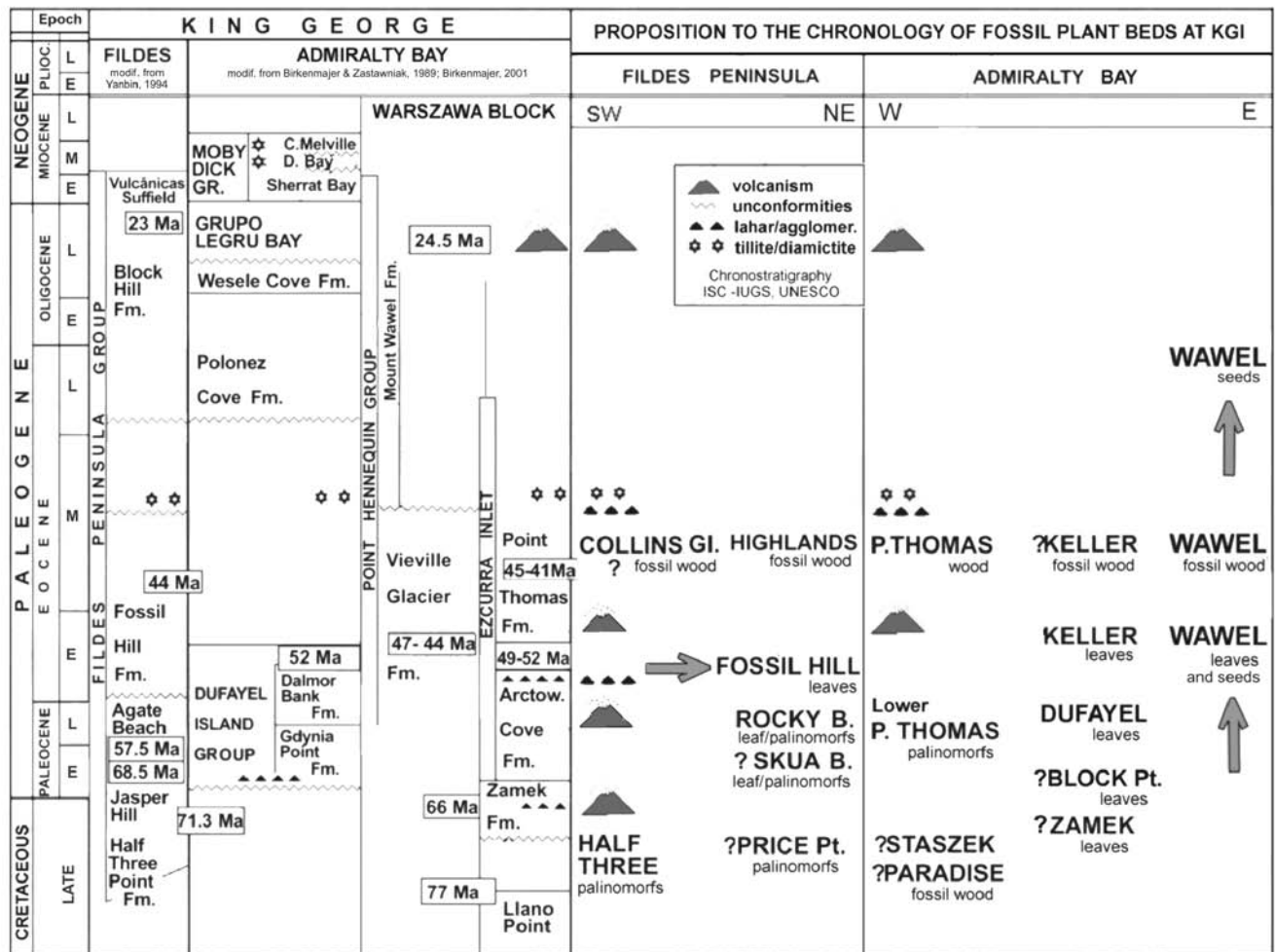
Figure 7. Proposed age and relative position of the plant fossils assemblages from the south (Fildes Peninsula) and central parts (Admiralty Bay) of King George Island (modified from Dutra, 2004). The arrows indicate where plant assemblages were found along with reproductive structures of Podocarpaceae. Radiometric ages from Birkenmajer *et al.* (1986), Soliani Jr. *et al.* (1988) and Yinxi & Yanbin (1994). Tectonically and volcanic induced deposits follow those proposed by Birkenmajer (2001). Glacial influenced lithologies (tilittes) based on Santos *et al.* (1994) and Birkenmajer *et al.* (2005).

The plants were studied using an Olympus Stereomicroscope with photographic and drawing devices. Images obtained were processed using Corel Draw 13. Other records of macrostructures were made with a Canon digital camera (10.2 Mpx resolution) and the measurements were taken with a precision device. SEM analysis and cuticle preparations were carried out but provided no additional data.

Plant remains were compared with published descriptions of modern analogs and herbarium sheets housed at Universidade do Vale do Rio do Sinos (UNISINOS) in the Herbarium of the Instituto Anchietano de Pesquisas (IAC) and at the Paleontological Museum (comparative collection) of the Post-Graduation Program in Geology (NITGeo). The nomenclature used in the description of shoot and leaf morphology was that suggested by de Laubenfels (1969), Offler (1984) and Wells & Hill (1989). Comparisons with fossil material were made with published works focusing on similar fossils from the austral basins and Antarctic Peninsula. The samples described here are housed at the Paleontological Museum (sect. Antarctica) at UNISINOS, in São Leopoldo city, Rio Grande do Sul State, Brazil.

SYSTEMATIC DESCRIPTIONS

Division CONIFEROPHYTA
Class GYMNOSPERMOPSIDA
Order CONIFERALES
Family PODOCARPACEAE Endlicher, 1847

Dacrydium vel *Halocarpus*
(Figures 8A-D)

1981 *Dacrydium* vel *Dacrycarpus* Zastawniak; p. 101-102, pl. 2, fig. 3.

Material. Impressions and charcolified compressions of 43 fragments, one referring to a more complete apical branch (ANTF MW-023) and the others to parts of the shoots (ANTF MW-004a to 004j, ANTF MW-019a to 019f, ANTF MW-055a to 055c, ANTF MW-060, ANTF MW-064a, ANTF MW-080a to 080c, ANTF MW-091, ANTF MW-133 Aa and Ba, 133 Ab and Bb, 133 Ac and Bc, 133 Ad and Bd, ANTF MW-008, ANTF MW-031, ANTF MW-010, ANTF MW-025A, ANTF

MW-006, ANTF MW-009a to 009d, ANTF MW-020a, ANTF MW-001, ANTF SZ-006).

Holotype. ANTF MW-023, level C (Figure 4).

Locality. Middle part of Mount Wawel succession, at Admiralty Bay, KGI.

Stratigraphic unit. The levels were assigned to the Point Hennequin Group of Hawkes (1961). The plant remains, first described from moraine deposits (Wanda Glacier and "Smok Hill plant beds") and from Szafer, are now attributed to volcanoclastic and volcanic beds located at ~ 90 m above sea level (Figure 4).

Age. Early Eocene.

Description. Apical shoot and isolated parts of helically to sub-opposite arranged leaf twigs, with planar insertion (angles of 45º), 1-2 mm wide, with mostly broad, imbricate scale-like leaves, giving way along the shoots and in some branchlets to a more linear shaped, falcate, slightly spreading and incurved ones. Bifacial leaves 1-2 mm in length and 0.5-1 mm wide, ranging from (short) diamond-shape types to more elongate and unguiform, with free and blunt apices and adnate bases narrow. Abaxial keels or midvein absent.

Discussion. The form and general morphology of these shoots with leaves varying in form and imbrications along the shoot are both very similar to those from the *ex-situ* material from the "Dragon Glacier plant beds" commented on and figured by Zastawniak (1981), and assigned without a formal description to *Dacrydium* vel *Dacrycarpus*. These are supplemented by additional specimens and associated with its original stratigraphic level. Other morphotypes of *Dacrydium* (e.g. *D. araucarioides*) from the Mount Wawel beds have also been suggested by Zastawniak (1981).

Following the works of Quinn & Gadek (1981) and Quinn (1982), regarding the relationships within *Dacrydium* s.l. and the erection of *Dacrydium* sect. B and C, the taxonomic placement of these fossils, and those described by Zastawniak (1981), can be refined. Considering the records mentioned, the combination of a foliage morphology characterized by diamond-shaped imbricate leaves, with distinct forms and arrangements, which give way to more elongated, spreading and incurved ones at the shoot apices, confirm the relation to the genus *Dacrycarpus* but a more proximal affinity with *Halocarpus,* rather than *Dacrydium* vel *Dacrycarpus*, as suggested by Zastawniak (1981).

Within modern species of *Halocarpus,* this foliage type can be found in *H. bidwillii*, where the development of the typical keel that characterizes the other species of the genus is also not common. According to Quinn & Gadek (1981) and Quinn (1982), the slender and planar disposed shoots, with spirally to sub-opposite scale-like and heterophyllic leaf shoots characterize members of *Dacrydium* section C, which includes *Halocarpus* (especially *H. bidwilli* Quinn, formerly *Dacrydium bidwilli*). Today, mature foliage of *Halocarpus* and *Dacrydium* differs only by the more abrupt change from one leaf type to the other. This occurs without transition in *Halocarpus* (Eckenwalder, 2009).

The absence of anatomic features and the current global deficit in macrofossils attributable to *Halocarpus* (rather than to "*Dacrydium* sp."), prevents certain placement within one of these two modern genera. In light of recent phylogenetic work, it is therefore timely for a revision of the austral podocarpaceous plant fossil record (see Pole, 1997) to determine whether closer taxonomic relationships can be made between fossil and extant taxa.

Further support for the presence of *Halocarpus* in the fossil record of KGI comes from an isolated and incomplete seed (see discussion below) found in associated levels at Mount Wawel (Figure 8G), which shows evidence of a striated epimatium similar to that found in extant forms of the genus. However, one isolated pollen cone with size and morphology very similar to those found in *Dacrydium cupressinum* Solander *ex* G. Forst., 1786 is also present (Figures 8E,F). These reproductive structures are useful in providing evidence for the presence of the Podocarpaceae at Mount Wawel, rather than Cupressaceae which can have a similar leaf shoot-morphology. Reproductive structures that could belong to the Cupressaceae are as yet unknown from this locality, although cupressaceous foliage forms an important contribution to the conifer component in the Fossil Hill assemblage, in Fildes Peninsula (Zhiyan & Haomin, 1994).

Within the pollen assemblage of Fossil Hill, at Fildes Peninsula, *Dacrydium* related forms are also present with the pollen grains of *Trisaccites* and *Dacrydiumites florinii*, most closely associated with modern *D. cupressinum* (Torres & Méon, 1990; Cao, 1992; Dutra & Batten, 2000).

On Snow Hill Island (eastern Antarctic Peninsula), fossil forms described from the Upper Cretaceous, such as *Sequoia fastigiata* (Sternberg) Nathorst (Halle, 1913), also share morphological characteristics with the extant species *Dacrydium colensoi* Hook. and *D. intermedium* Kirk. In Late Cenozoic beds of both southern Victoria Land and erratic blocks of McMurdo Sound, East Antarctica, *Dacrydium* remains are often found associated with *Nothofagus* (Francis *et al.*, 2008).

In South America, pollen grains of *Dacrydiumites florinii* are represented in beds spanning the Upper Cretaceous to Miocene, associated with macrofossils of *Dacrydium* (Fasola, 1969; Romero, 1986; Troncoso & Romero, 1993). *Dacrydiumites* becomes increasingly frequent within Neogene strata of those areas that formerly made up East Gondwana. However, detailed taxonomic abundances at the genus level need to be reconsidered in light of advances in podocarp systematics. In New Zealand and across eastern and southeastern Australia, including Tasmania, the macroflora and palynological assemblages indicate that *Dacrydium*, *Dacrydium/Podocarpus*, *Dacrydium* group B, and *Parvisaccites catastus* Stover & Partridge, a type thought to be related to extant *Halocarpus* (ex *Dacrydium) bidwillii/ kirkii* and *D. biforme,* have been present throughout much of the Cenozoic (Pocknall, 1981; Macphail *et al.*, 1994; Hill & Christophel, 2001).

Halocarpus bidwillii is today a dwarf frost-resistant Podocarpaceae, exclusive to New Zealand, where it occurs from Cape Colville on the Coromandel Peninsula, to Stewart Island, and between 600-1,500 m in elevation in the north, but at lower altitudes nearer to sea level in the south. It is hardy, growing in both bogs and dry stony ground, usually in montane to subalpine scrub (Eckenwalder, 2009). In the west coast of the South Island, *H. bidwillii* grows in mixed temperate rainforest under a canopy dominated by
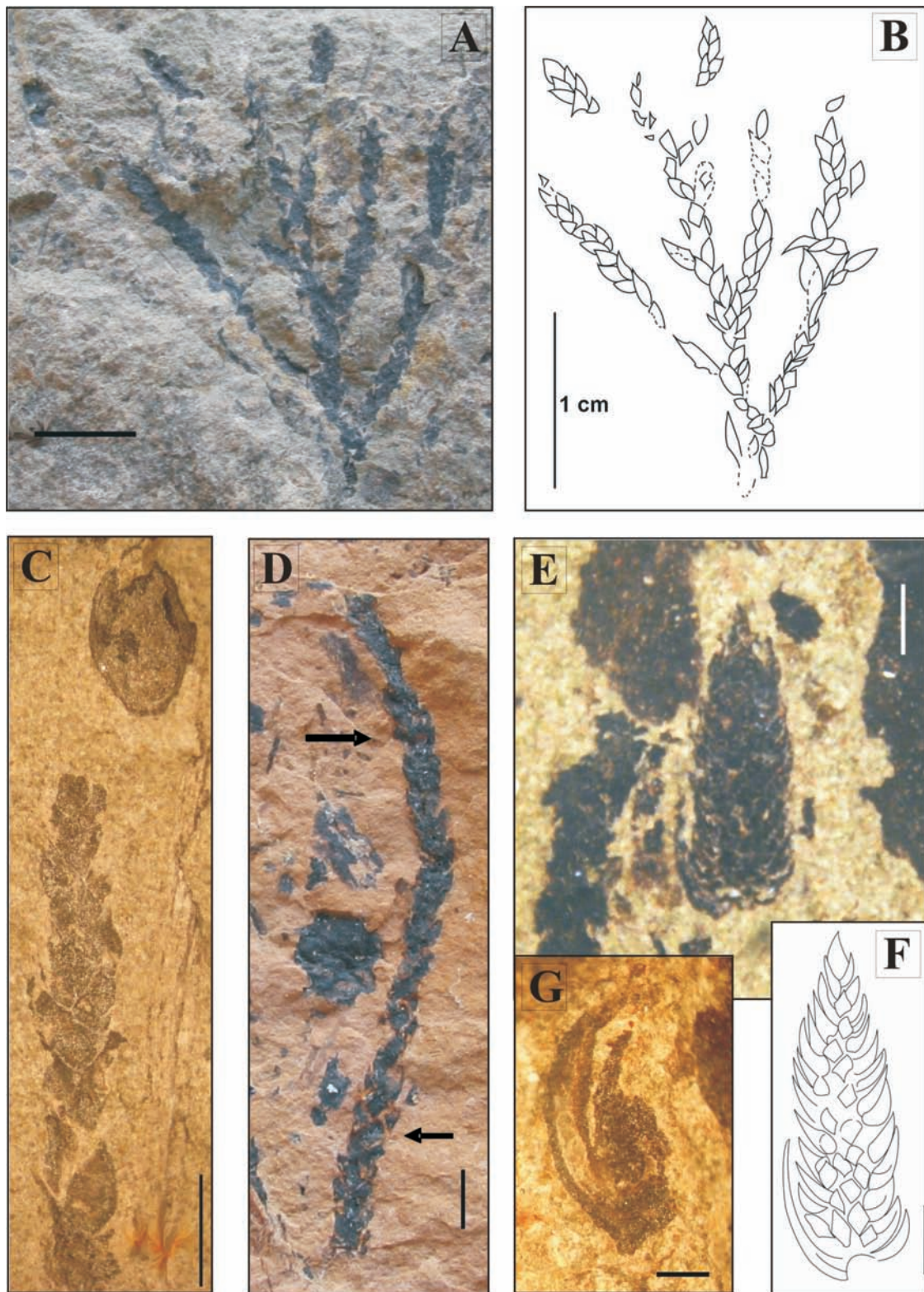
Figure 8. A-D, Apical leaf shoots of *Dacrydium* vel *Halocarpus* from Mount Wawel: **A**, bifacial flattened shoots, with planar and alternate insertion and spiral to sub-opposite arranged imbricate leaves (sample ANTF MW-023, scale bar= 10 mm); **B**, drawing in camera lucida from A to show detail; **C**, detail of an apical branchlets exhibiting adpressed, diamond-shaped leaves (from level C of the Mount Wawel profile). The flat and isolated seed at upper right exhibits a morphology similar to that found in *H. bidwilli* and *D. cupressinum*, and the broken part could suggest predation by insects (ANTF MW-063, scale bar= 2 mm); **D**, detail of an apical branch showing the distinct sizes and form of leaves (arrows) in basal and upper part of the shoot (ANTF MW-010, scale bar= 2 mm); **E-F**, isolated small pollen cone, similar to those of extant *D. cupressinum* (scale bar= 2 mm); **G**, ovalate and flattened seed with size similar to those of extant *Halocarpus bidwilli* and *Dacrycarpus dacrydioides*. In modern *D. dacridioides*, similar breakage features are observed following drying of the seed (ANTF MW-063, scale bar = 0.5 mm).

Dacrydium cupressinum (the rimu), the same taxa inferred by the isolated cone in associated beds on KGI. The composition and diversity of this modern biome, comprising *Nothofagus*, diversified Podocarpaceae and ferns, is in part very similar to that preserved in the Mount Wawel paleoassemblage. The difference between the modern flora and the assemblage of Mount Wawel flora is the presence of *Araucaria* remains, along with other angiosperm exhibiting affinities to the nowadays South American region (Boardman & Dutra, 2005), which confers a mixed character to the taphoflora.

Genus *Dacrycarpus* (Endl.) C.J. Quinn, 1982
Dacrycarpus tertiarius n.comb.
(Figures 9A-D)

1928 *Fitzroya tertiaria* Berry; p. 13, pl. 2, figs. 2-4.
1938 *Fitzroya tertiaria* Berry; p. 60, pl. 12, fig. 2.
1940 *Podocarpus tertiarius* (Berry) Florin; p. 39.
1981 *Dacrycarpus dacrydioides* (Zastawniak, pl. 2, figs. 1-3).
1994a *Podocarpus tertiarius* (Berry) Florin, 1940; Zhou Zhiyan & Li Haomin, pl.1, figs. 5-8a; text-fig. 2.
1996 *Dacrycarpus*? *tertiarius* (Berry) Zastawniak (*in* Doktor *et al.*), p. 133-134, pl. 32, fig. 1.

Material. Impressions of apical and medial portions of four vegetative shoots, sometimes covered by charcolified material (ANTF 35-002, ANTF 35-001, ANTF 35-005, ANTF 35-007).
Holotype. ANTF 35-002, basal levels of the fossiliferous interval at the top of Fossil Hill.
Locality. Fossil Hill succession, Fildes Peninsula, KGI.
Stratigraphic unit. Fossil Hill Formation (Yanbin, 1994), Fildes Peninsula Group (Hawkes, 1961).
Age. ?Late Paleocene to Early Eocene.
Description. Elongated and slender shoots with dominant planar, sometimes alternate disposition, 1 mm wide, branchlets inserted at angles varying from 35º to 45º (1-0.8 mm wide). Bifacial and appressed scale-like leaves, helically arranged (2 + 3 to 1 + 2 parastichies) and slightly spreading, with a short acute to obtuse free portion, and well-developed wide adnate and decurrent base. The uniform leaf sizes (1.5 to 2.5 mm in length, 0.8 to 1 mm wide) only varies to little more elongated ones in the proximal part of the branches. No keels apparent.
Discussion. The disposition of the shoots coupled with heterophyllic slightly spreading bifacial and appressed leaves, with wide decurrent adnate bases dominant over the free apices (form A from Offler, 1984), include those impressions in the range of variation found in mature foliage of the modern genus *Dacrycarpus*.

Zhiyan & Haomin (1994a, pl.1, figs. 5-8a; text-fig. 2) described fossil remains with similar morphology from the same beds as those discussed here, and formally proposed a relation to *Podocarpus tertiarius* (Berry) Florin, which is discussed here.

This morphotype was first discovered in Chile by Florin (1940), and was identified as having closest morphological similarity to extant *Pherosphera* and *Dacrydium*. Later, Orlando (1964) and Czajkowski & Rösler (1986) found similar morphologies in shoots preserved in equivalent beds on Fossil Hill, at KGI.

New material found during the course of this study, with foliage morphology very similar to that described and figured by Zhiyan & Haoamin (1994a), shows branches and branchlets with planar ramifications suggesting a close similarity to members of the genus *Dacrycarpus* rather than *Podocarpus* (*cf.* de Laubenfels 1969), which have leaves normally short petiolate and bifacial flattened (Form E from Offler, 1984). Therefore, the new generic combination *Dacrycarpus tertiarius* is proposed here, highlighting the morphological similarity of the fossil remains with *Dacrycarpus* mature foliage (Figure 9A). It also shares a common morphology with the leaf shoots assigned to *Dacrycarpus*? *tertiarius,* from the La Meseta Formation on Seymour Island by Zastawniak (Doktor *et al.*, 1996), as well as those from Southern Chile referred to as *Podocarpus dacrydioides* A. Rich. by Florin (1931), and with *Fitzroya tertiaria* and *P. tertiarius,* respectively, as described by Berry (1928, 1938) and Florin (1940) from the Lower Eocene beds of the Chalia and Pichileufú rivers in Patagonia (Romero, 1986).

The incomplete nature of the fossils, in particular the lack of preserved cuticle, prevents further taxonomic determination. However, noteworthy is the similarity between these fossils and the mature foliage of extant *D. dacrydioides* (A. Rich.) de Laub. Moreover, the presence in the Mount Wawel beds of two seeds with morphology and size very similar to that of *Dacrycarpus* (Figure 9G) and a juvenile shoot of *D. dacrydioides* (Zastawniak, 1981, plate 2, fig. 1) heightens the evidence for the presence of *Dacrycarpus* in the Antarctic at this time.

Dacrycarpus related forms are also present since the Middle Jurassic in the pollen assemblages (*Dacrycarpites* spp.) of South America (Martínez, 2002) and in the Upper Cretaceous, together with leaf impressions and woods, in Antarctica, New Zealand and Australia. By the end of the Paleogene, it seems to have disappeared from the southern South American region, more or less coeval with its disappearance from the northern Antarctic Peninsula (Dettmann & Jarzen, 1990; Askin, 1990).

The quantity of fossils assigned to *Dacrycarpus* from the Eocene to Miocene of Australia and from the Miocene of New Zealand make those areas the only ones to surpass in abundance those found in the Paleogene of the northern Antarctic Peninsula (Wells & Hill, 1989; Pole, 1998; Hill & Whang, 2000). In Australia, some Miocene forms were related to *Dacrycarpus elandensis* Hill & Whang, which shares morphological similarity to the modern species *D. imbricatus*, whilst others appear more related to *D. dacrydioides* (de Laubenfels, 1988; Pole, 1992; Carpenter *et al.*, 1994).

In Southern Australia, *Dacrycarpus* maintained its diversity until the arrival of the severe cold, dry climate that characterized the Lower Pleistocene, when the retreat of the rainforest gave way to the arrival of *Eucalyptus* forests (Hill & Carpenter, 1991; Jordan, 1995; Hill & Whang, 2000).

Today *Dacrycarpus* has a broad geographical distribution across the eastern areas of the Southern Hemisphere, in forests from South China to Fiji, New Guinea (where it has its greatest variety and number of species) and across to New Zealand. Except in the last country, where it is broadly dispersed, its distribution is restricted to the eastern sides of
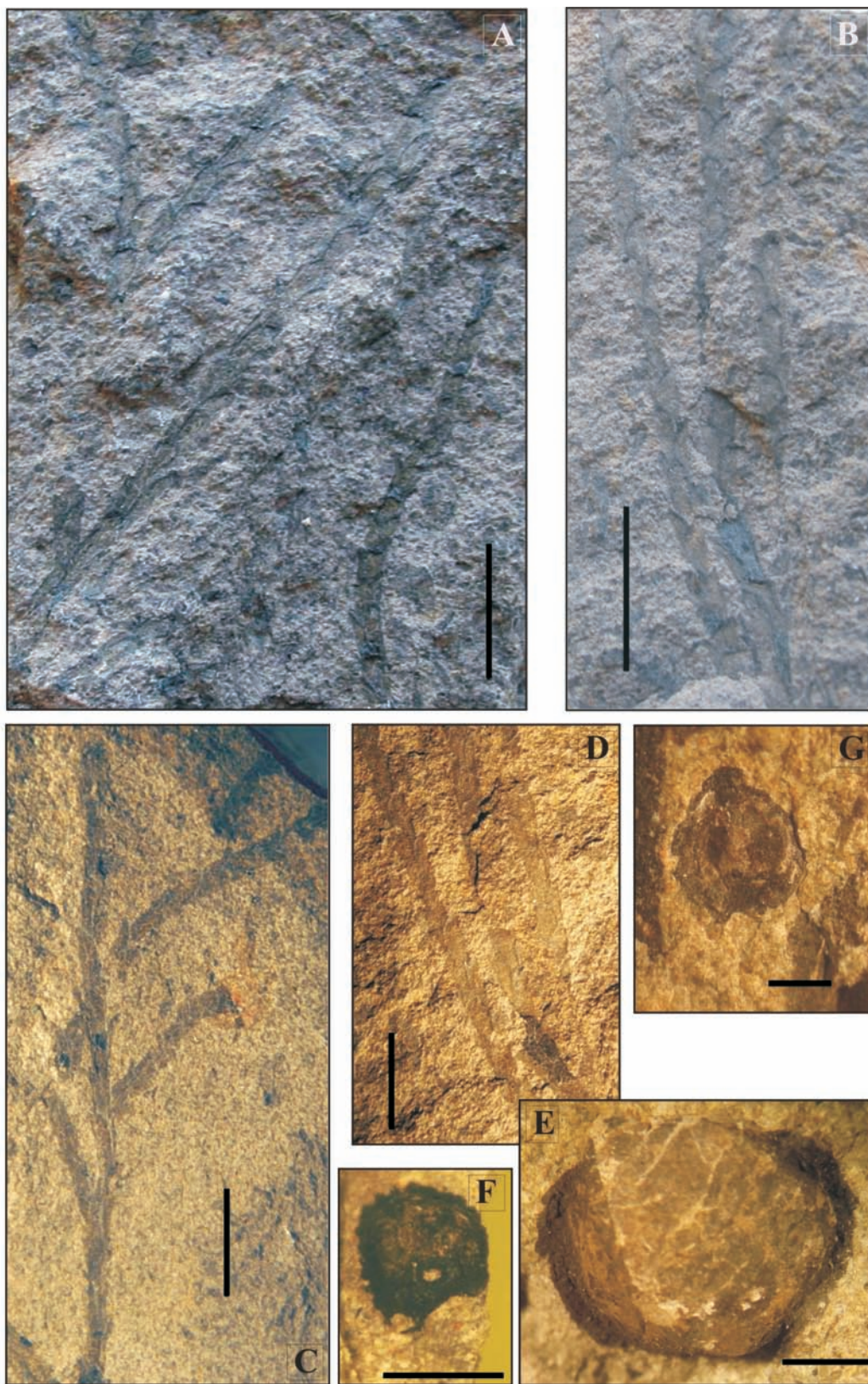
Figure 9. A-D, Apical branch and branchlets of *Dacrycarpus tertiarius* n.comb., originating from the upper most plant assemblage at Fossil Hill, Fildes Peninsula (Figure 2), showing the slender leaf shoots and short imbricate leaves: **A-B**, holotype (sample ANTF 35-002, scale bar= 10 mm); **C**, aspect of the foliage showing the planar and alternate insertion in slender shoots (ANTF 35-001, scale bar= 10 mm); **D**, detail of the spiral to sub-opposite, ovalate and imbricate leaves (ANTF 35-005, scale bar= 10 mm). **E-G**, isolated seeds from level A of Mount Wawel: **E**, isolated seed (ANTF MW-014A, scale bar= 10 mm) similar to *Carpolites* sp. 1 of Zastawniak *et al.* (1985); **F**, round seed similar to that found in modern *Dacrycarpus* species and in *Lepidothamnus intermedius*, with wrinkled testa or epimatium (ANTF MW-016, scale bar= 2 mm); **G**, incomplete and detached seed, also with affinity to those found in modern *Lepidothamnus* genus (ANTF MW-063, scale bar= 1 mm).

the land masses where wet oceanic climates prevail. The species *D. dacrydioides* is now restricted to New Zealand, where it dominates in stature and grows on the fertile soils of flood plains and low terraces of fluvial basins (de Laubenfels, 1988; Blanchon, 2005). *D. dacrydioides* can also grow up to an altitude of 600 m, where it adopts a shrub habit, especially on South Island, New Zealand (Cubitt & Molloy, 1994). In south Westland, it contributes to the lowland forest that characteristically comprises *Dacrydium cupressinum*, *Prumnopytis ferruginea* and *Weinmannia racemosa,* colonizing mineral-rich and silty soils resulting from intense flood disturbance (Duncan, 1993).

SEEDS

A diversity of dispersed seeds related to the Podocarpaceae has previously been found in the *in-situ* "Mount Wawel beds" by Zastawniak *et al.* (1985). They assigned these seeds to *Carpolites* spp., and related them to *Podocarpus* sect. *Stachycarpus.* Similar forms also occur in extant members of the genera *Falcatifolium, Acmopile* and *Prumnopytis* (Eckenwalder, 2009). In the studied material described here, other distinct seeds were found and between them, only one exhibits a size (5 mm long) similar to that described by those authors (Figure 9E).

The other seeds here originate from the basal-most levels (Level A, Figure 4) and include two main morphotypes. They are either rounded or flattened, and some have parts of the epimatium preserved, which suggests morphological similarity to *Dacrycarpus* and *Dacrydium* (Eckenwalder, 2009). Modern podocarp seeds show a strong degree of similarity, and therefore, it is not always possible to pinpoint their affinities, but the small seeds identified here can be subdivided further based on morphological characters. Those flattened and with an apparently resistant testa, complete with longitudinal striations, is common to modern *Dacrydium* and its segregated genera, such as *Manoao, Halocarpus* (e.g. *H. bidwilli*) or *Lagarostrobus* (Figure 8C,G). Interestingly, the kind of fragmentation exhibited in one of them (Figure 8C) suggests possible evidence for plant-insect interaction. Similar features can be seen in modern detached seeds of *D. cupressinum* following germination. The type of fragmentation, with characteristic jagged edges, could attest to the action of weta insects (Family Stenopelmatidae), as they break the seed coats (Beveridge, 1964).

The second morphotype, with more rounded appearance, apical protuberances and sometimes with a low crest, is more suggestive of *Dacrycarpus* (e.g. *D. dacrydioides*), *Prumnopytis* or *Lepidothamnus* (Figures 9F,G).

The presence of these reproductive structures serves to strengthen evidence for the presence of the family Podocarpaceae at KGI during the Paleogene, supported also by previous works. The associated depositional features (ichnofossils, mud cracks and rain drops) provide information regarding their probable transport from high areas, prior to deposition in ephemeral and shallow lakes.

FINAL COMMENTS

The shoots covered by short, imbricate and bifacial leaf types and the seeds found in the Paleogene strata of KGI provide good evidence for the presence of podocarps growing across the hilly slopes and in lowland coastal areas, during periods of quiescence, or at a time preceding volcanic activity. The fragmentary and disconnected nature of the plant remains, dominated by parts of apical shoots also indicates a parauthoctonous (*e.g.* Fossil Hill) and allochthonous (in middle to upper Mount Wawel fossiliferous intervals) nature of deposition, respectively, through either transportation in ephemeral rivers and deltas or from surge processes that coincided with the beginning of a new period of volcanic activity (*e.g.* level C, from Mount Wawel deposition).

Otherwise, the assemblage at Fossil Hill, due to its greater abundance in *Podocarpus* spp. and other needle-leaf shoots, ferns and broader and bigger (~12 cm long) leaves of *Nothofagus* seems to reflect an environmental context distinct from that of probably coetaneous Mount Wawel basal levels. Here, the imbricate leaf types related to *Dacrydium* s.l. are more diverse and abundant and are accompanied by *Araucaria* representatives, Dicksoniaceae ferns and numerous *Nothofagus,* which have smaller leaf sizes. This would suggest that at least one assemblage originated from slopes or higher areas, subject to a little colder or drier conditions, which is supported by the paleoclimatic data derived from wood and leaf analyses. The values obtained at the end of the Paleocene and Lower Eocene for KGI in fossil wood ring and leaf margin analyses, indicates a mean annual temperature (MAT) in the range of about 12°C or 13°C, respectively for the Mount Wawel and Fossil Hill localities, similar to the values obtained from the Early Eocene levels from James Ross and Seymour Islands, where the MAT is thought to have been about 13.5°C (Poole *et al.*, 2005). Yet, with regard to mean annual precipitation (MAP), the Mount Wawel floras appear to have experienced drier conditions (~950 mm), while the Fossil Hill locality seems to have been much wetter (~1730 mm). At this moment, Seymour Island, located on the eastern side of the Antarctic Peninsula, appears to have experienced precipitation levels similar to those observed today in south Brazil and the Valdivian region in Chile (*i.e.* ~2311 mm). It suggests that probably the westerly system of winds that now have a great influence over the humidity in the area, had not yet established or had little influence during the end of the Paleocene and early Eocene times.

The more continuous succession from Mount Wawel (levels A to D) and the upward impoverishment of flora and the reduction in leaf sizes (*e.g. Nothofagus* related forms), support the proposition of an initial drastic drop in regional temperatures dating back to the beginning of Middle Eocene (Birkenmajer *et al*., 2005; Ivany *et al*., 2008). Today, the modern podocarp relatives whose remains have been found at these upper levels exist in wet, cold habitats over mountains and/ or near sea in higher latitudes. This confirms the podocarps' resistance to cold climate which characterized Antarctica after post-Middle Eocene times, documented by the *in-situ* seeds found on the top of Mont Wawel.

Taking into account the structural complexity of the lithologies at KGI, these podocarp-rich marker horizons are useful for the establishment of the stratigraphic framework across the KGI. Moreover, it may also be possible to use the most diversified plant horizons (in Fossil Hill and middle alti-

tude of Mount Wawel) and the floristic nature of the assemblages to synchronize deposits on KGI with those in the upper part of the Cross Valley Formation, or with the lower part of La Meseta Formation on Seymour Island, which suggests a time between the end of the Paleocene (Fossil Hill) through the beginning of the Middle Eocene (Mount Wawel succession). In the last place, it expresses a discrepancy with the stratigraphic model proposed by Birkenmajer (2001), which could be attributed to the *ex-situ* nature of the fossil assemblages at the time of his works, and/or to the alleged complex structural character of the island.

The imbricate-leaved podocarps discussed here show morphologies very similar to those of extant *Dacrydium* (or *Halocarpus*) and *Dacrycarpus*, found today on oceanic islands across the eastern flank of the Southern Hemisphere, especially South and Stewart Islands (New Zealand). Therefore mainly the modern biomes in the last islands (located at higher latitudes and where both taxa occur) may prove to be a good living analogue for the ecological context, as well as providing a more detailed understanding of the climatic conditions that presided over King George Island between the end of Paleocene and lower part of the Eocene. The association of these podocarps with other plant remains, some of them with clear affinity to taxa now living in South America, can also contribute to our understanding of the importance of coastal environments around Antarctica for the origin and/or distribution of the modern vegetation in the Southern Hemisphere.

ACKNOWLEDGMENTS

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