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Nothofagus and the associated palynoflora from the Late Cretaceous of Vega Island, Antarctic Peninsula

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Abstract: Nothofagaceae fossil leaves and an associated palynoflora from Late Cretaceous sediments of Vega Island, eastern Antarctic Peninsula, are presented. The leaves are described as *Nothofagus* sp. 1 and Morphotype LDB 1, and come from the Snow Hill Island (late Campanian-early Maastrichtian) and the López de Bertodano (late Maastrichtian) formations, respectively. The palynoflora obtained from levels immediately above and below the *Nothofagus* sp. 1 and in the same horizon as the Morphotype LDB 1, included terrestrial and marine elements. In the palynoflora associated with *Nothofagus* sp. 1, conifers are dominant and pollen grains with *Nothofagus* affinity are represented by four species: *Nothofagidites kaitangataensis* (Te Punga) Romero 1973 and *Nothofagidites senectus* Dettmann and Playford 1968, which belong to the ancestral pollen type, as well as *Nothofagidites dorotensis* Romero 1973 and *Nothofagidites* sp. of the *brassii*-type. Cryptogamic spores, marine dinoflagellate cysts and algae, among others, are part of the assemblage. The palynoflora associated with the Morphotype LDB 1 also contains abundant conifer and angiosperm pollen grains with *N. dorotensis* as the only *Nothofagus* species recorded. Marine dinoflagellate cysts are scarce while fungi and phytodebris are common elements. The joint presence of marine and non-marine palynomorphs supports a probable nearshore environment at time of deposition for both units. Pollen and spore evidence suggests a mixed conifer and angiosperm forest, with Podocarpaceae and *Nothofagus* as the main components, and ferns, lycopods, and mosses in the understory. This forest developed under temperate and moist conditions during the middle Campanian-Maastrichtian.

Key words: Antarctica, Vega Island, Cretaceous, Nothofagaceae leaves, palynology.

Introduction

Nothofagus Blume, the southern beech, is the only genus of the family Nothofagaceae (Order Fagales) and comprises 35 species living in Argentina, Chile, Australia, New Zealand, New Guinea, and New Caledonia (*e.g.*, Hill and Jordan 1993; Hill and Dettmann 1996; Sauquet *et al*. 2012). *Nothofagus* species are usually dominants in the temperate forests where they grow (*e.g.*, Glade-Vargas *et al*. 2018). Their fossil record is extremely abundant and consists of leaves, wood, reproductive structures, and pollen grains, in the areas mentioned above, as well as in the Antarctic Peninsula (*e.g.*, Dettmann and Thomson 1987; Dutra and Batten 2000; Hayes *et al*. 2006; Poole and Cantrill 2006; Kvaček and Vodrážka 2016; Cantrill 2018).

The role of the Antarctic Peninsula as a locus of early evolution of *Nothofagus* has been discussed for many years. Cranwell (1964), Askin (1989) and Dettman (1989) discussed an Antarctic origin for *Nothofagus* pointing out that Antarctica and closely associated areas of southern South America and southern Australasia were the site of origin of several floral elements including *Nothofagus*. The radiation centre of the genus was close to the northern Antarctic Peninsula (Cantrill and Nichols 1996). Its origin goes back to the Coniacian (Reguero *et al*. 2013) while its diversification took place during the late Campanian and Maastrichtian (Hill and Dettmann 1996). Pollen evidence, represented by the genus *Nothofagidites*, also indicates evolution in southern high latitudes, having synchronous early Campanian appearances in West Antarctica, New Zealand, and South Australia, although the precise centre of origin in Antarctica or surrounding areas has not been defined. Subsequent dispersion and diversification in temperate areas of other continents were also suggested (*e.g.*, Dettmann *et al*. 1990; Glade-Vargas *et al*. 2018).

The oldest known record of *Nothofagus* or related leaves goes back to the Coniacian of Hidden Lake Formation, James Ross Island, eastern Antarctic Peninsula (EAP), and consists of a poorly preserved fragment of a small leaf assigned to cf. *Nothofagus* sp. (Kvaček and Vodrážka 2016). Other mentions of Nothofagaceae leaves are from the Santa Marta Formation (Santonian – early Campanian) that outcrops on James Ross Island (Vega and Olivero 1992; Hayes *et al*. 2006). In younger Maastrichtian rocks from López de Bertodano Formation

(Sandwich Bluff Member), Vega Island, several *Nothofagus*-like leaves have been reported but no descriptions were provided and only one specimen has been illustrated (Roberts *et al*. 2014). In western Antarctic Peninsula (WAP), on Nelson Island and King George islands, Campanian – early Maastrichtian *Nothofagus* leaf morphotypes have also been found (Cao 1994; Bastos *et al*. 2013).

Although several reports on angiosperm leaves have been published, the Antarctic Cretaceous flora, and in particular, well-preserved *Nothofagus* leaves, have not been adequately described. Antarctic Nothofagaceae leaves still deserve further investigation.

Early history of *Nothofagus*, however, can also be deduced from the ancestral pollen grains of *Nothofagidites endurus* Stover and Evans 1973 and *N. senectus* Dettmann and Playford 1968, recorded from the late Campanian to Maastrichtian sediments from the James Ross Basin, EAP (*e.g*., Dettmann *et al*. 1990; Dolding 1992; Keating 1992) and *N. endurus* and *N. kaitangataensis* (Te Punga) Romero 1973 in the Campanian – early Maastrichtian strata from Nelson Island, WAP (Bastos *et al*. 2013).

The aim of this paper is to document the presence of well-preserved Nothofagaceae leaves in Late Cretaceous sediments of Snow Island and López de Bertodano formations, exposed at Cape Lamb, Vega Island, EAP, and to describe the features that may shed light on the taxonomy and evolution of this iconic genus. Looking for a paleofloristic, paleoenvironmental and biostratigraphic control, the associated pollen grains and other palynomorphs recovered from the same strata or close stratigraphic levels (above and below) as the leaves are also studied. Analysis of the micro-and megaflora obtained from the same levels is rare in the Late Cretaceous of the Antarctic Peninsula area and only a few studies are known from the WAP (*i.e*., Dutra and Batten 2000; Bastos *et al*. 2013).

Geological setting and paleontology

Cretaceous strata at Cape Lamb, Vega Island (Fig. 1A–B) are included in the Marambio Group, with ages varying between the late Campanian to late Maastrichtian. The thickness of the Cretaceous section is *ca*. 462 m. Its base is not exposed and the top is unconformably overlaid by Cenozoic glacial diamictites and volcanic rocks from the James Ross Volcanic Group, JRVG (Marenssi *et al*. 2001).

Crame *et al*. (1991) carried out regional stratigraphy of the Cretaceous outcrops of Cape Lamb. They described three informal units named as A, B, and C, later formalized into three units: 1 – the Herbert Sound Member of the Santa Marta Formation; 2 – the Cape Lamb Member of the Snow Hill Island Formation; and 3 – the Sandwich Bluff Member of the López de Bertodano Formation (Pirrie *et al*. 1997). Alternatively, Marenssi *et al*. (2001) divided this entire

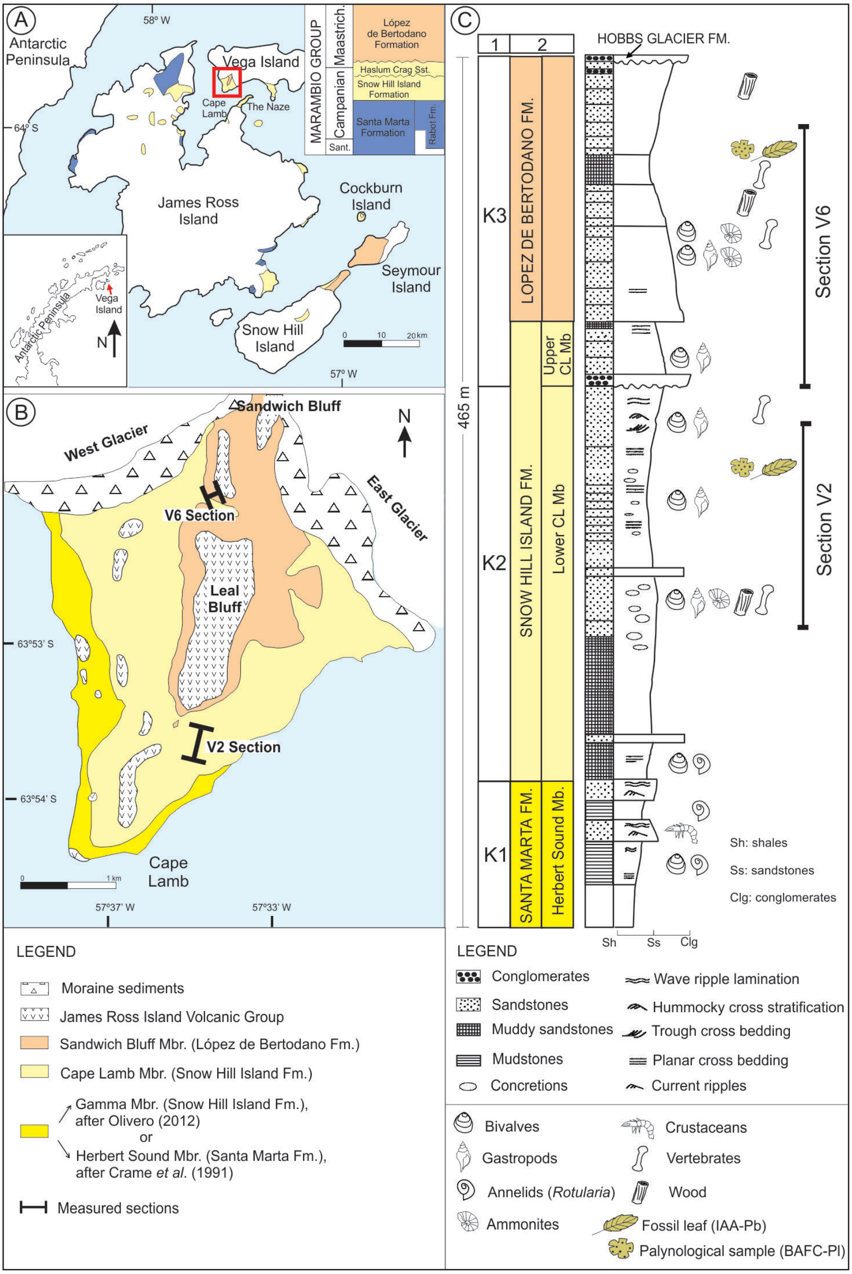

Fig. 1. **A.** Location map of Vega Island, eastern Antarctic Peninsula, showing outcrop distribution of Upper Cretaceous units of the James Ross Basin (after Olivero 2012). **B.** Geological map of Cape Lamb, Vega Island, indicating V2 and V6 sections (after Marenssi *et al.* 2001). **C.** Integrated lithological log of Cape Lamb (after Marenssi *et al.* 2001) with location of the studied leaves and palynological samples and invertebrate, vertebrate and wood fossils (after Marenssi *et al.* 2001). 1 – informal units proposed by Marenssi *et al.* (2001); 2 – Stratigraphy proposed by Roberts *et al.* (2014).

Cretaceous sedimentary section into three informal stratigraphic units named as K1, K2, and K3 (Fig. 1C). They are composed of poorly consolidated sandstones, silty sandstones, siltstones, mudstones, and a well-defined conglomerate bed that represent two complete transgressive-regressive cycles. Cesari *et al*. (2001) suggested equivalence between the units defined by Pirrie *et al*. (1997) and Marenssi *et al*. (2001), pointing out that the lower member K1 is equivalent to the Herbert Sound Member of the Santa Marta Formation and K2 correlates with the lower part of the Cape Lamb Member of the Snow Hill Island Formation. The unit K3 comprises the upper part of the Cape Lamb Member and the Sandwich Bluff Member of the López de Bertodano Formation (Fig. 1C). Olivero (2012) incorporated the Gamma Member, which was originally defined for the uppermost sediments of the Santa Marta Formation (Olivero *et al*. 1986), into the Snow Hill Island Formation and indicated that the member is approximately equivalent to the Herbert Sound Member of Crame *et al*. (1991).

Subsequently, Roberts *et al*. (2014), in their exhaustive revision of the Upper Cretaceous stratigraphy of the Cape Lamb, established that Unit K2 of Marenssi *et al*. (2001) corresponds to the lower Cape Lamb Member (lower CL Mb) of the Snow Hill Formation (Fig. 1C), which was deposited in an upward-shallowing, mid- to outer-shelf setting. However, Olivero (2012) interpreted it as a progradational deltaic wedge. Unit K3 of Marenssi *et al*. (2001) was included by Roberts *et al*. (2014) in the upper Cape Lamb Member (upper CL Mb) and the Sandwich Bluff Member (SB Mb) of the López de Bertodano Formation (Fig. 1C) and they proposed a mid- to outer shelf setting, as part of a transgressive system tract for the upper CL Mb while SB Mb would represent a nearshore marine to possibly terrestrial, upward coarsening siliciclastic succession.

The lower CL Mb of the Snow Hill Island Formation yield abundant and diverse marine invertebrates such as ammonoids, nautiloids, bivalves, gastropods, crustaceans, and serpulid worms (*e.g*., Pirrie *et al*. 1991; Olivero 2012; Roberts *et al*. 2014), and a vertebrate fauna that includes fragments of sharks and marine reptiles (Marenssi *et al*. 2001; Reguero *et al*. 2013). The flora consists of silicified podocarp-like wood, typically heavily perforated by *Teredolites* borings, and an araucarian ovulate cone (Césari *et al*. 2001). Palynomorphs have been also recovered from this unit and consist of pollen, spores and dinoflagellate cysts (Pirrie *et al*. 1991; Smith 1992).

The upper CL Mb of the Snow Hill Island Formation has a similar content of marine invertebrates to that of the lower CL Mb. They are more common in the base of the upper CL Mb and decrease in abundance and diversity upwards (Roberts *et al*. 2014). The SB Mb of the López de Bertodano Formation has a more abundant and diverse fauna than the underlying upper CL Mb. Among the vertebrate fossils, the best known discoveries are an anseriform bird (Reguero *et al*. 2013) in the middle part of the SB Mb, marine reptiles (mosasaur and plesiosaur) and an hadrosaurid dinosaur found at the "Reptile Horizon" (Case *et al*. 2000, Reguero *et al*. 2013) in the upper third of the SB Mb. The flora consists of unidentified angiosperm leaves and seeds and *Nothofagus*-like leaves found in the lower levels of the SB Mb (Roberts *et al*. 2014). Araucarian leaves (Césari *et al*. 2001), abundant fossil wood logs and carbonaceous plant hash were also recognized in the upper levels of SB Mb (Roberts *et al*. 2014). Palynological assemblages are also recovered from this member (Dettmann and Thomson 1987; Pirrie *et al*. 1991).

Material and methods

During the 2000–2001 summer season expedition, two different composite sections were measured at Cape Lamb. The complete sedimentary sequence is 465 m thick (Fig. 1C), with the strike ranging from 5° to 40° NNE, and 4° SE dip. Slumps and slides are frequent in the Cape Lamb area making the accurate measurement of the Cretaceous sedimentary beds difficult. The two analyzed sections, named V2 and V6 (Fig. 1B–C), are three kilometres apart.

Section V2 (63°53’19.7” S; 57°36’2.5” W) coincides with unit K2 of Marenssi *et al*. (2001) or to the lower CL Mb of Snow Hill Island Formation of Roberts *et al*. (2014). It is 113 m thick and is characterized by brown silty sandstones, green-brown fine sandstones, and an indurated olive green fine-grained bed (7 cm thick) from where the two leaves occur. They were collected from a layer equivalent to the level where Césari *et al*. (2001, Fig. 1, locality A) found the araucarian silicified wood and cone.

Section V6 (63°51’43.3” S; 57°34’17.3” W) is 78 m thick and coincides with unit K3 of Marenssi *et al*. (2001) or to the upper CL Mb of Snow Hill Island Formation and the SB Mb of López de Bertodano Formation of Roberts *et al*. (2014). It consists of green-grey sandstones, intercalated with indurated green marls, siltstones, and very thin bentonite claystone. One fossil leaf comes from an indurated bentonite bed equivalent to the level where the hadrosaurid dinosaur was found (Case *et al*. 2000), and above the fossil podocarpacean leaves studied by Césari *et al*. (2001).

The three fossil leaves recovered from the sections V2 and V6 are incomplete or fragmentary. They unfortunately lack cuticle, however they have well-preserved margins and high order venation allowing their taxonomic determination.

Palynological assemblages were recovered from three samples: two of them come from levels above and below the fossil leaf from V2 section and the third one comes from the same level as the fossil leaf of Section V6. They were extracted from the rocks using palynological procedures that consisted of extracting organic matter by digesting the carbonates and silicates with respectively, HCl and HF. The residue was sieved with 25 µm and 10 µm meshes and mounted on microscope slides with glycerine jelly (Wood *et al*. 1996).

Fossil leaves were described following the terminology of Hickey (1973), LAWG (1999) and Ellis *et al*. (2009). Spore and pollen nomenclature follows that of Halbritter *et al*. (2018) and the taxonomy of dinoflagellate cysts is in accordance with Williams *et al*. (2017).

Fossil leaves are housed in the Repository of the Instituto Antártico Argentino (IAA), Argentina, as IAA-Pb 539, 540a, 540b, and 541. Palynological slides are stored in the Palynological Collection of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (FCEN-UBA), Argentina, under the acronym BAFC-Pl and the slide numbers 1486 (1–10), 1629 (1–3), and 1630 (1–3). Observations were made with a Leitz M5 stereomicroscope and a Nikon 80i microscope at the FCEN-UBA. The photomicrographs were taken with a Nikon Coolpix 950 digital camera.

Fossil leaves

The fossil leaves collected from Section V2 show detailed morphology of veins and margin, and one of the specimens is fairly complete, so it is possible to identify them as belonging to the genus *Nothofagus*. We describe the material as *Nothofagus* sp. 1, and relationships with other records of *Nothofagus* from the Late Cretaceous of the Antarctic Peninsula area are discussed.

The single specimen collected from Section V6 is a piece of a broken fossil leaf, with excellent preservation of high order venation. We describe this form as Morphotype LDB 1, in reference to the López de Bertodano Formation.

When discussing relationships to subgenera, we follow to the concepts of Hill and Read (1991) and Hill *et al*. (2015)

Order Fagales Engler
Family Nothofagaceae Kuprianova
Genus *Nothofagus* Blume
Nothofagus sp. 1
(Fig. 2A–K)

Studied material. — (2 specimens) IAA-Pb 539, IAA-Pb 541.

Geographic occurrence. — Section V2 (63° 53’19.7” S; 57° 36’2.5” W), Cape Lamb, Vega Island, Eastern Antarctic Peninsula.

Stratigraphic occurrence. — Lower Cape Lamb Member of the Snow Hill Island Formation.

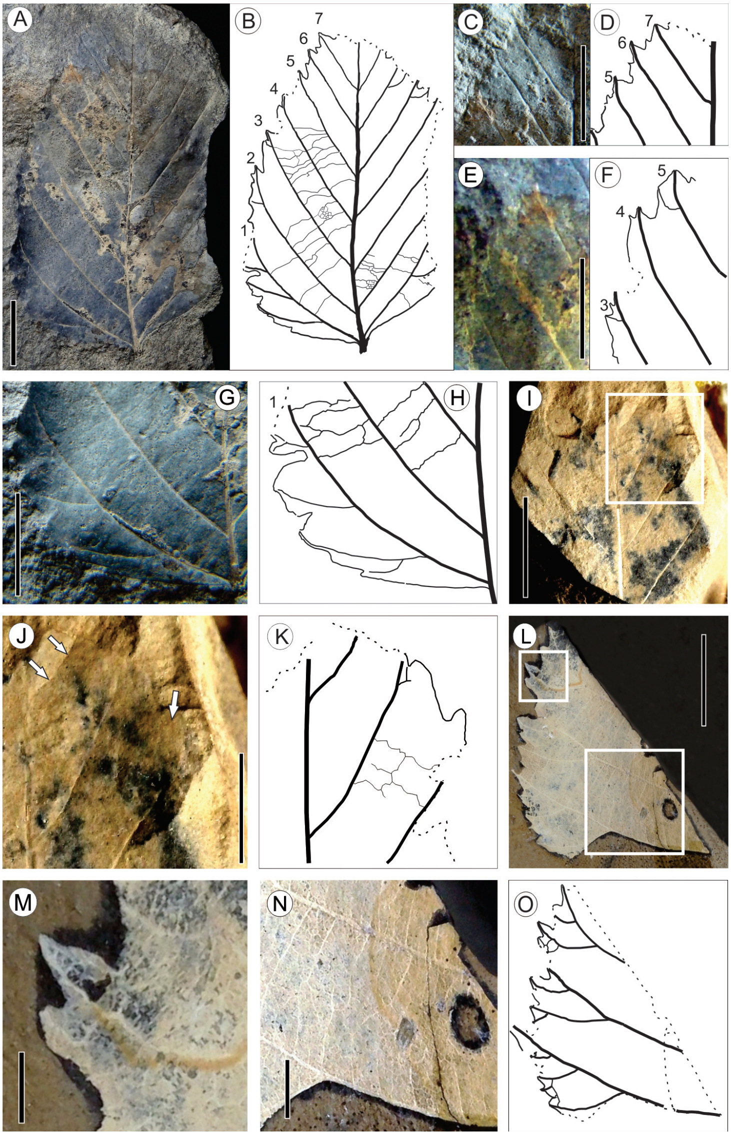

Fig. 2. Fossil leaves recovered from the lower CL Mb of the Snow Hill Island Formation (Section V2) and the SB Mb of the López de Bertodano Formation (Section V6), Cape Lamb, Vega Island, EAP. **A–H.** *Nothofagus* sp. 1, Specimen IAA-Pb 539. **A–B.** Complete specimen, photo and line drawing showing the seven (numbers 1–7) secondary veins. **C–D.** Detail of an apical area of the margin, with the 5 to 7 secondary veins. **E–F.** Margin with secondary veins 3 to 5. **G–H.** Marginal basal part of the leaf with the first secondary vein. **I–K.** *Nothofagus* sp. 1, Specimen IAA-Pb 541. **I.** Complete specimen. **J–K,** Apical area, photo and line drawing. Note arrows pointing slight plicate lamina along the uppermost secondary vein. **L–O,** Morphotype LDB 1, Specimen IAA-Pb 540a. **L, O.** Part of the leaf specimen and line drawing. **M.** Upper left square in L, detail of damage margin, note branch of secondary and high order venation abruptly cut. **N.** Lower right square in L, detail of high order venation, note opposite and alternate percurrent third, and reticulate fourth order venation, detail of damage. Scale bars in J–K 2 mm; L–O 5 mm; others 10 mm.

Description. — The leaf lamina is simple, microphyll, about 42 mm long and 28 mm wide, symmetrical, broadly ovate. Base obtuse, asymmetrical, concave-convex. Apex acute, straight. Margin serrate. Teeth compound, with one principal tooth and 1–2 accessory teeth, more numerous towards the base. Teeth regularly spaced, 1–2 per cm in the middle of the leaf, with acute apical angles, variable in shape, wide and convex-convex type of serration in the base of the leaf, slender and straight-straight towards the apex. Sinuses rounded, wide in the middle of the leaf, narrow in the leaf base. The main sinus, which separates two compound teeth, usually just above each secondary vein. Petiole normal, 1 mm long preserved. Pinnate, simple craspedodromous secondary venation. Primary vein moderate and straight, becoming thinner towards the apex. Eight pairs of secondary veins, subopposite, thin, emerging at a moderate acute angle of 50°, with a parallel and slightly curved course, more abrupt close to the margin, and entering directly and eccentrically in the main tooth of the compound teeth along its basal side. Two basal veins on one side of the leaf emerge at a wider angle and have a more curved course than the ones in the same pair on the other side, and have compound agrophic veins, so contributing to the asymmetry of the base. Intercostal areas irregular, curved or very slightly folding. Tertiary veins preserved only in a few intercostal areas, percurrent, mixed opposite/alternate, emerging mostly at right angles from the secondaries, and forming a uniform obtuse angle of about 130° with the primary vein inconsistently, but sometimes emerging at wider angles. Fourth order veins preserved in patches, regular polygonal reticulate. Leaf texture probably chartaceous. The lamina is fairly flat, but a couple of intercostal areas are slightly curved.

Comments. — Leaf specimen IAA-Pb 539 (Fig. 2A–H) is preserved as an impression, and lacks about 10% of the apex and most of the right side margin, but has a well-preserved base and left side margin. Specimen IAA-Pb 541 (Fig. 2I–K) shows part of a badly preserved lamina, with only the midvein and four pairs of suboposite, straight secondary veins. The apex, base and high order venation are not preserved. The margin may be found only along a small part of the right side, were two teeth are visible. Intercostal areas are slightly plicate (Fig. 2J, indicated by arrows) that can be seen when illuminating a secondary vein from the apical side. The basal side of the secondary vein becomes shadowed; the light-dark contrast is possible because of the slight plication of the lamina along the secondary vein.

Morphotype LDB 1
(Fig. 2L–O)

Studied material. — (1 specimen) IAA-Pb 540a, 540b

Geographic occurrence. — Section V6 (63°51’43.3” S; 57°34’17.3” W), Cape Lamb, Vega Island, Eastern Antarctic Peninsula.

Stratigraphic occurrence. — Sandwich Bluff Member of the López de Bertodano Formation.

Description. — The specimen is a part of a leaf, including margin and basal venation, but lacking midvein and half of the leaf. Margin serrate. Teeth compound, with one principal tooth and 2–3 accessory teeth, which are more numerous towards the base. Teeth regularly spaced, with acute apical angles, wide and convex-convex type of serration. Sinuses rounded, narrow. The main sinus, which separates two compound teeth, usually just above each secondary vein. Simple craspedodromous secondary venation. Primary vein not preserved. Three secondary veins preserved, with a parallel and slightly curved course, entering directly and eccentrically in the main tooth of the compound teeth along the basal side of the tooth. The three secondaries have agrophic veins, the two basal ones with compound agrophic veins. Tertiary veins percurrent, mixed opposite/alternate, emerging mostly at right angles. Fourth order veins regular, thin, reticulate. Fifth order regular, thin, reticulate. Areoles polygonal, well-developed, small. Veinlets no well-preserved, apparently bifurcating once.

Comments. — The specimen is broken, and has a counterpart. High order venation and marginal features are enhanced by a thick white mineral coating similar to that described in Césari *el al*. (2001). The margin is damaged in parts (Fig. 2L–M), and the sediment alongside the margin is stained with a dark colour (Fig. 2M). It is similar to damage DT 114, in Labandeira *et al*. (2007), which is described as a necrotic tissue strip along the leaf margin. Furthermore, close to the midvein, there is a circular insect damage with a dark brim of reaction necrotic tissue (Fig. 2N) similar to DT 148 of Labandeira *et al*. (2007).

Close comparison between the description of *Nothofagus* sp. 1 and that of Morphotype LDB 1 shows that they are identical in any character that is preserved in both taxa. The only character that could make an exception is the number of accessory teeth, which is 1–2 in *Nothofagus* sp. 1 and 2–3 in Morphotype LDB 1, although this could be a variable character. *Nothofagus* sp. 1 is based in a fairly complete specimen with details of venation, and a second, broken specimen. LDB 1 is based in a very fragmentary, though well-preserved specimen. Of course, no comparison can be done with missing characters in one of the taxa, but preserved characters in both taxa, such as margin, secondary, tertiary and fourth order veins would suggest that both belong to the same species. We have not followed that way, however, considering that the specimens were found in sediments of two different formations, separated by several millions years, and that the material is scarce and fragmentary. Further collections may shed light on this assignation.

Comparison with other Late Cretaceous *Nothofagus* leaf records from the Antarctic Peninsula area. — The specimen cf. *Nothofagus* sp. described by Kvaček and Vodrážka (2016: fig. 7K), from the Coniacian Hidden Lake Fm, James Ross Island, EAP, is a small leaf fragment with simple dentate/crenate margin, craspedodromous venation and percurrent tertiary veins. The illustrated specimen shows four rounded crenate teeth and a very small sinus, different from the marginal features of both forms herein described (*Nothofagus* sp. 1 and Morphotype LDB 1). The characters of the Hidden Lake leaf observed by Kvaček and Vodrážka (2016), however, are present in several living species of *Nothofagus*, such as *N. moorei* (F. Muell) Krasser, *N. dombeyi* (Mirb.) Oerst and *N. nitida* (Phill.) Krasser (Gandolfo and Romero 1992: figs 13–15; Hill and Read 1991: figs. 56–58 and 64–67).

The specimens studied by Hayes *et al*. (2006) are described as "morphotypes with architectural characteristics typical of the Cunoniaceae and Nothofagaceae", and unfortunately there are no photos of the specimens. The line drawings show only gross leaf morphology of primary and secondary veins, therefore it was impossible to establish informative comparisons with the herein described material.

In sediments of the Coniacian–Santonian age at Hanna Point, Livingston Island, WAP, Leppe *et al*. (2007) reported and illustrated a flora dominated by ferns and gymnosperms, with only two records of angiosperms. One of them (Angiosperm form 1, fig. 2D in Leppe *et al*. 2007) has craspedodromous venation, and could be related to *Nothofagus*. However, the margin is poorly preserved and the absence of tertiary or higher order venation precludes accurate comparisons.

In King George Island (25 de Mayo), several floras with *Nothofagus* species were described, in sediments of the Zamek Formation, originally considered late Campanian–Maastrichtian (Birkenmajer and Zastawniak 1989; Dutra and Batten 2000). Also, in the very close Nelson Island, Bastos *et al*. (2013) described a flora very similar to those of King George Island, with several morphotypes related to *Nothofagus*, in a volcanoclastic succession. They suggested a late Campanian age for the flora although no litho or chronological units were defined.

Recent radiometric dating in several localities on King George Island suggested an early to middle Eocene age for the Zamek Formation (Cantrill 2018; Mozer *et al*. 2015).

However, there is a reasonable doubt about the age of the sediments of Nelson Island, because radiometric sampling was not made on this Island, and the palynoflora documented by Bastos *et al*. (2013) includes Late Cretaceous gymnosperms (*Classopollis simplex* and *Cycadopites* aff. *C. follicularis*) and primitive pollen of *Nothofagidites* (*Nothofagidites asperus* Romero 1977, *N. endurus, N. kaitangataensis* and ancestral group b of Dettmann *et al*. 1990). Therefore, the age of the sediments of Nelson Island remains controversial. Thus, we decided to compare our material with several morphotypes of Nelson Island, and *Nothofagus* species from the Zamek Formation in King George Island.

Three species of *Nothofagus*, based on leaf characters, were formally proposed on materials from the Zamek Formation (Zawstawniak 1994; Dutra and Batten 2000) and five morphotypes were defined by Bastos *et al*. (2013) for Nelson Island. All of them are based on features of gross morphology (size, primary and secondary veins, sometimes tertiary veins). As far as gross leaf morphology allows, we only found some resemblances between *Nothofagus* sp. 1 and *Nothofagus cretacea* Zastawniak 1994, from Zamek Formation, in size of the lamina, number of secondary veins, their angles of emergency, and their slightly curved course. However, more material with more detailed morphology (*i.e.,* leaf margin and the venation pattern) should be found to establish a proper comparison.

Bastos *et al*. (2013) described five morphotypes (RIP 5 to RIP 9) in the "*Nothofagus* (protophilic) Group" from late Campanian sediments from Rip Point, Nelson Island. All of them differ from *Nothofagus* sp. 1 mainly in shape and size, and course of the primary and secondary veins. Morphotype RIP 7 is the most similar because of comparable size and number of secondary veins. That morphotype has also partially preserved percurrent tertiary veins, although they are opposite and sinuous, not opposite straight and alternate as in *Nothofagus* sp. 1.

Therefore, none of the mentioned records of *Nothofagus* can be closely compared to our material. Most of them are based on gross morphology which precludes fair comparisons. Base, apex, margin, and third and higher order venations are absent in most of the published material and those features are the diagnostic characteristics, thus they are the most important for comparing *Nothofagus* leaves, both in extant and fossil specimens as several authors have previously pointed out (Hill 1983; Tanai 1986; Hill and Read 1991; Gandolfo and Romero 1992; Jordan and Hill 1999; Vento *et al*. 2016; Glade Vargas *et al*. 2018). The specimen of Kvaček and Vodrážka (2016) and the ones described herein, although being fragmentary, show detailed morphology of the leaves that allows placement within *Nothofagus*.

The fossils from Vega Island show a few features that are not present in living *Nothofagus* or in fossil ones, taking into account what has been published so far. They are: the irregular spacing of secondary veins, which results in irregular intercostal areas; the angle of tertiary veins with the primary vein, which is obtuse, but not consistently, because sometimes tertiary veins emerge at wider angles; the differences in the margin between the apical and the basal parts, like the shape of teeth and the width of sinus between base and apex. Several of these characters define a Second Rank vein system (LAWG 1999). If better preserved material confirms these features, it could be possible that the fossils from Vega Island belong to an ancestral, extinct Cretaceous clade, in the sense of the Ancestral Group defined on the basis of pollen grains (Dettmann *et al*. 1990).

Comparison with *Nothofagus* living species. — The well-preserved high-order venation in the material herein described allows comparison with living species. Serrate margin with compound teeth and rounded sinuses, and an asymmetrical base with agrophic veins are characters of *Nothofagus* sp. 1 and Morphotype LDB1 that are also in numerous species of living *Nothofagus*, as it was mentioned by several authors such as Hill (1983), Tanai (1986), Hill and Read (1991), Gandolfo and Romero (1992), Jordan and Hill (1999), among others. Most of these authors agree that these basic features may be found in *Nothofagus glauca* (Phil.) Krasser, *Nothofagus obliqua* (Mirb.) Oerst., and *Nothofagus alpina* (Poepp. and Endl.), plus *Nothofagus alessandrii* Espinosa which is sometimes added to these three species on the basis of particular features (*e.g.*, composite teeth, principal sinus adjacent to principal teeth, more than six secondary veins among others). Tanai (1986) groups *N. glauca* (Phil.) Krasser, *N. obliqua* (Mirb.) Oerst. and *N. alpina* (Poepp. and Endl.) Oerst. on the basis of relative size and the course of the secondary vein when reaching the tooth (straight and along the basal side of the tooth). These are features present in our material. Jordan and Hill (1999) discussed variations in the course of the main and accessory veins in the tooth of those four species, and also the course of branches of the secondary, that reach subsidiary teeth, as in *Nothofagus* sp. 1 from Vega Island. Gandolfo and Romero (1992) pointed out the presence of composite teeth and ovate shape, and more than six pairs of secondary veins in the above mentioned four living species. They differentiate *N. obliqua* by having basal secondary veins with branches only on one side of the leaf reinforcing the asymmetry of the leaf, as may be seen in *Nothofagus* sp. 1. *Nothofagus obliqua* and *N. glauca* have 7–10 secondary veins and percurrent tertiary veins dominantly alternate and opposite, respectively, and *Nothohagus* sp. 1 has both kinds of tertiary veins in the same leaf. However, *N. glauca* has an asymmetrical base and agrophic veins as in *Nothofagus* sp. 1. Also, Gandolfo and Romero (1992) remarked that *N. alpina* and *N. alessandrii* share a high number of secondary veins (10–15), higher than *Nothofagus* sp. 1, but the former has a principal sinus, which separates two composite teeth, just below each secondary vein, while the second has that sinus just above each secondary vein, as is observed in *Nothofagus* sp. 1 and Morphotype LDB 1.

Therefore, if some relationship could be established between *Nothofagus* sp. 1 and Morphotype LDB 1, on the one hand, and living *Nothofagus* species, on the other, it should be within this discussed group of species. *Nothofagus obliqua, N. alpina* and *N. glauca* belong to the deciduous group of species in the subgenus *Lophozonia*, and *N. alessandrii* belongs to the subgenus *Fuscospora* (Hill and Jordan 1993).

Palynology

A palynological assemblage was recovered from Section V2 (lower CL Mb of Snow Hill Island Formation) from a sample (BAFC-Pl 1629) immediately above the level containing the fossil leaf BAFC-Pl 539 (Table 1, Figs 1 and 3). It provided both terrestrial and marine well-preserved palynomorphs, some of them containing pyrite crystals (Fig. 3M and V). The land-derived elements

Table 1

List of palynomorphs recovered from the lower CL Mb of Snow Hill Island Formation (Section V2) and SB Mb of the López de Bertodano Formation (Section V6), Cape Lamb, Vega Island, EAP. Section V2: sample BAFC-Pl 1629: above the fossil leaf IAA-Pb 539; sample BAFC-Pl 1630: level below the fossil leaf IAA-Pb 539. Section V6: sample BAFC-Pl 1486, the same bed as fossil leaf IAA-Pb 540a, b. Botanical affinity after Raine *et al*. (2011). Abbreviations: SHI Fm (Snow Hill Island Formation); LdB Fm (López de Bertodano Formation); lower CL Mb (Cape Lamb Member); SB Mb (Sandwich Bluff Member).

PALYNOMORPHS	SHI Fm.		LdB Fm.	Fig.
	Lower CL Mb		SB Mb	
	V2		V6	
	BAFC-Pl 1629	BAFC-Pl 1630	BAFC-Pl 1486	
Spores				
Bryophyta				
Stereisporites antiquasporites (Wilson and Webster 1946) Dettmann 1963	X	X		3.J
Lycophyta				
Ceratosporites equalis Cookson and Dettmann 1958	X			
Retitriletes austroclavatidites (Cookson) Döring, Krutzsch, Mai and Schulz 1963	X	X	X	3.I
Pteridophyta				
Baculatisporites comaumensis (Cookson) Potonié 1956			X	
Cyathidites australis Couper 1953	X			
Laevigatosporites ovatus Wilson and Webster 1946	X			
Peromonolites sp.			X	
Gymnospermous pollen				
Araucariaceae				
Callialasporites trilobatus (Balme) Dev 1961 (possibly reworked)			X	
Podocarpaceae				
Microcachryidites antarcticus Cookson 1947	X	X	X	3.G
Phyllocladidites mawsonii Cookson ex Couper 1953	X	X	X	3.F
Podocarpidites spp.	X	X	X	3.H
Trichotomosulcites subgranulatus Couper 1953	X	X		

PALYNOMORPHS	SHI Fm.		LdB Fm.	Fig.
	Lower CL Mb		SB Mb	
	V2		V6	
	BAFC -Pl 1629	BAFC -Pl 1630	BAFC -Pl 1486	
Angiospermous pollen				
Fagaceae				
Nothofagidites dorotensis Romero 1973	X	X	X	3.A
Nothofagidites kaitangataensis (Te Punga) Romero 1973	X	X		3.B
Nothofagidites senectus Dettmann and Playford 1968	X	X		3.C
Nothofagidites sp. (*brassii*-type)	X	X		3.D–E
Nyssaceae				
?*Nyssapollenites* sp.	X			
Gunneraceae				
Tricolpites reticulatus Cookson ex Couper 1953	X			
Proteaceae				
Forcipites sabulosus (Dettmann and Playford) Dettmann and Jarzen 1988	X		X	
Lewalanipollis sp. cf. *L. senectus* Dettmann and Jarzen 1996	X			
Peninsulapollis askiniae Dettmann and Jarzen 1988	X		X	
Peninsulapollis gillii (Cookson) Dettmann and Jarzen 1988	X	X	X	3.R
Peninsulapollis truswelliae Dettmann and Jarzen 1988		X	X	3.S
Proteacidites subscabratus Couper 1960		X		
Propylipollis sp. A Dettmann and Thomson 1987			X	
Triporopollenites sp.	X			
Tricolporites sp.			X	
Unknown extinct angiosperm				
Tricolpites sp.			X	
Fungi				
Callimothallus sp.			X	3.W
Colligerites sp.			X	3.X
Plochmopeltinites sp.			X	
Spores, hiphae and fruiting bodies			X	3.Y
Phytoclasts				
Podocarpaceous tracheids			X	3.T–U
Cuticles			X	
Dinoflagellate cysts				
Batiacasphaera reticulata (Davey 1969) Davey 1979	X	X		3.O
Impletosphaeridium clavus (Wrenn and Hart 1988)	X	X	X	3.P-Q
emend. Bowman, Riding, Francis, Crame and Hannah 2013	X	X		3.M
Isabelidinium pellucidum (Deflandre and Cookson 1955) Lentin and Williams 1977	X	X		3.N
Operculodinium radiculatum Smith 1992	X	X		3.K
Odontochitina porifera Cookson 1956		X		
Spiniferites ramosus (Ehrenberg1838) Mantell 1854		X		3.L
Xenascus plotei Below 1981				
Other marine palynomorphs				
Microforaminiferal linings	X			
Palambages sp.		X	X	3.V

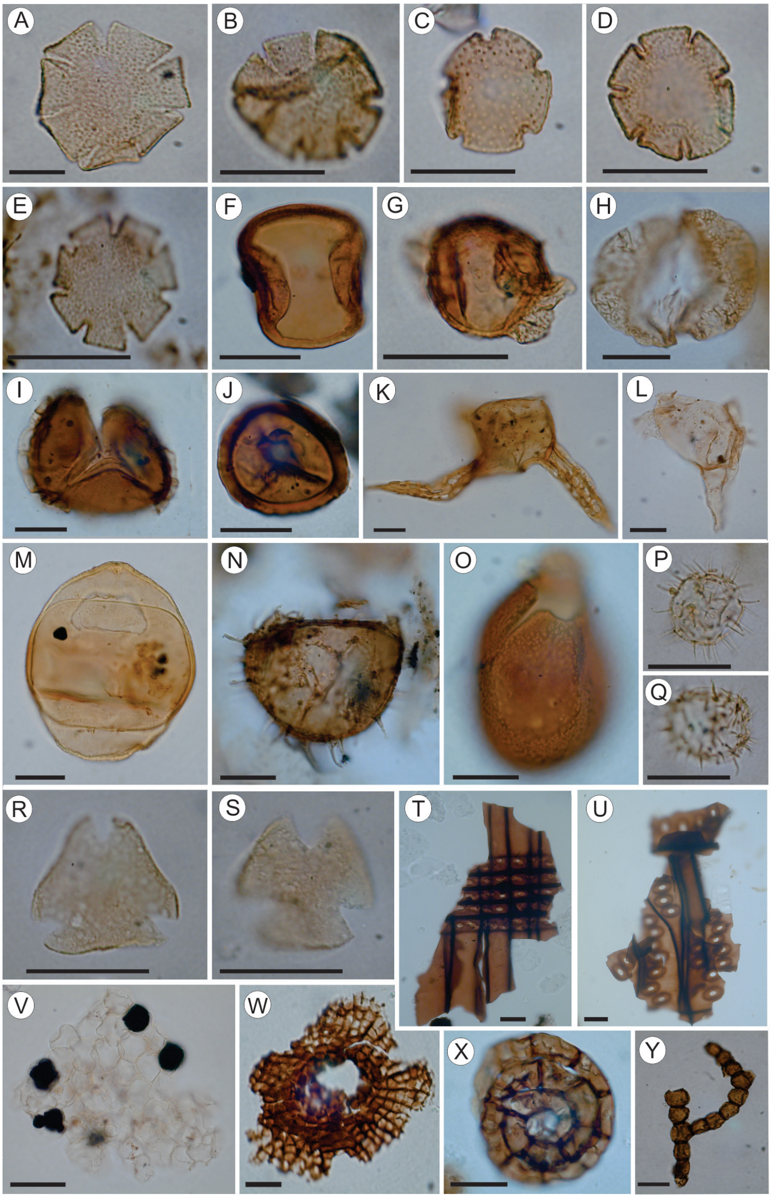

Fig. 3. Palynomorphs recovered from the lower CL Mb of Snow Hill Island Formation (Section V2) and SB Mb of the López de Bertodano Formation (Section V6), Cape Lamb, Vega Island, EAP. England Finder coordinates are given for each specimen after the repository name and sample number. Section V2: **A.** *Nothofagidites dorotensis*, BAFC-Pl 1630(2): Y47/3. **B.** *Nothofagidites kaitangataensis*, BAFC-Pl 1630(2): R47/4. **C.** *Nothofagidites senectus*, BAFC-Pl 1629(1): 49/3. **D.** *Nothofagidites* sp., *brassii*-type, BAFC-Pl 1629(1): Q33/3. **E.** *Nothofagidites* sp. *brassii*-type, BAFC-Pl 1629(1): R32/3. **F.** *Phyllocladidites mawsonii*, BAFC-Pl 1630(2): G31. **G.** *Microcachrydites antarcticus*, BAFC-Pl 1630(2): U39/2. **H.** *Podocarpidites* sp. BAFC-Pl 1630(2): P24. **I.** *Retitriletes austroclavatidites*, BAFC-Pl 1630(1): 41/3. **J.** *Stereisporites*

consist of conifer and angiosperm pollen grains, with *Nothofagus* the most abundant. It is represented by four species including two listed as "N. ancestral type" in Dettmann *et al*. (1990): *Nothofagidites kaitangataensis* (Fig. 3B) and *N*. *senectus* (Fig. 3C); plus *N. dorotensis* (Fig. 3A), and *Nothofagidites* sp. (Fig. 3D–E) here assigned to "*Nothofagus brassii* type". The last mentioned species consists of pollen grains oblate, peritreme, densely and evenly granulate, with thin exine and rimmed U-shaped colpi, 23 to 27 µm in equatorial diameter. They are similar to the *Nothofagidites* sp. recorded by Dettmann and Thomson (1987, sample D.3122.3, fig. 6k) from Maastrichtian strata of López de Bertodano Formation, Vega Island, EAP. Along with *Nothofagidites,* there are other angiosperm pollen grains, mainly Proteaceae. Bryophytes, lycophytes, and pteridophytes spores are scarce. The marine elements include dinoflagellate cysts (*Batiacasphaera reticulata*, *Impletosphaeridium clavus*, *Isabelidinium pellucidum*, *Operculodinium radiculatum*, and *Odontochitina porifera*) and microforaminiferal linings (Table 1).

In Section V2, a palynological assemblage was also recovered from a sample (BAFC-Pl 1630) immediately below the level of fossil leaf BAFC-Pl 539 (Table 1, Fig. 3). The assemblage is similar, but less diverse, to that one found in the level above the fossil leaf (sample BAFC-Pl 1629). Conifer pollen grains are dominant. Among the angiosperms, *Nothofagidites* is present with the same four species as in sample BAFC-Pl 1629 and other angiosperms are represented mainly by Proteaceae. The small spiny dinoflagellate cyst *Impletosphaeridium clavus* is a conspicuous component of the marine assemblage, accompanied by the same dinoflagellate cysts species as in the abovementioned sample, plus two other species (*Spiniferites ramosus* and *Xenascus plotei*). Colonies of the marine algae *Palambages* sp. are also found.

The palynological assemblage obtained from Section V6 (SB Mb of López de Bertodano Formation), is derived from the same level (sample BAFC-Pl 1486) as the fossil leaf BAFC-Pl 540a, b (Table 1, Fig. 3R–Y). Among the terrestrial elements, conifer and angiosperm pollen are the most abundant. *Nothofagidites* is represented only by *N. dorotensis*, while Protecaeae are also recorded. Spores of bryophytes and lycophytes are a minor component. The gymnosperm pollen grain *Callialasporites trilobatus* (Table 1) is also found in

antiquasporites, BAFC-Pl 1629(1): U46/3. **K.** *Odontochitina porifera*, BAFC-Pl 1630(1): L42. **L.** *Xenascus plotei*, 1630(1): L23/2. **M.** *Isabelidinium pellucidum*, BAFC-Pl 1629(1): E29/2. **N.** *Operculodinium radiculatum*, BAFC-Pl 1629(1): P22. **O.** *Batiacasphaera reticulata,* Z42/3. **P–Q.** *Impletosphaeridium clavus*, **P.** BAFC-Pl 1630(2): Y27/3, **Q.** BAFC-Pl 1630(2): Y47/2. Section V6: **R.** *Peninsulapollis gillii*, BAFC-Pl 1486(1): H35/1. **S.** *Peninsulapollis truswelliae*, BAFC-Pl 1486(9): W20/3. **T.** Podocarpaceous tracheids showing circular uniseriate bordered pits, BAFC-Pl 1486(2): F44/5. **U.** Podocarpaceous tracheids showing cross-field pits, BAFC-Pl 1486(2): U40/1. **V.** *Palambages* sp., BAFC-Pl 1486(2): T27. **W.** *Callimothallus* sp., BAFC-Pl 1486(6): C54/4. **X.** *Colligerites* sp., BAFC-Pl 1486(2): P41/4. **Y.** Fungal spore in short chain, BAFC-Pl 1486(2): W39/4. Scale bar: K–L, T–U: 50 µm, the rest 20 µm.

the assemblage. This specimen is probably a reworked component due to its dark preserved color, which is suggestive of a possible thermal alteration as previously discussed by Dettmann and Thomson (1987). Abundant phytodebris are present in the sample. They consist of fragments of tracheids with uniseriate bordered pits that are circular and have a separate arrangement (Fig. 3T–U). The cross-field pitting is typically podocarpoid, with one or two oblique pits per field and consistent with the co-occurrence of podocarpaceous pollen. We note the presence of diverse fungal spores and fruiting bodies in the sample, most of them referable to Microthyriales and assigned as *Callimothallus* sp. and *Colligerites* sp. (Fig. 3W–Y). Marine palynomorhs include many specimens of *Palambages* sp. and a few specimens of *Impletosphaeridium clavus*. No other dinoflagellate cysts were found in the sample.

Discussion

Fossil leaves. — Cantrill (2018), among others, notes that the leaf record of *Nothofagus*, starting during the Coniacian, predates the appearance of *Nothofagus* pollen, in the early Campanian in the Antarctic Peninsula (*e.g.*, Dutra and Batten 2000; Reguero *et al*. 2013). Hill (2001) remarked that the four extant subgenera of *Nothofagus* have been distinct entities for many tens of millions of years and since they appeared, evolutionary change within *Nothofagus* has been slow although extinction events occurred. As discussed above, our material has features that remain in several living species, mainly belonging to the subgenera *Lophozonia* and *Fuscospora*. This could indicate that by the Maastrichtian some differentiation had already occurred, and the basic features of the subfamilies were being established.

Palynology. — The three studied palynological assemblages comprise taxa previously reported from Cretaceous sediments of the James Ross Basin (*e.g*., Dettmann and Thomson 1987; Askin 1989; Dolding 1992; Keating 1992; Bowman *et al*. 2012, 2013, 2014; di Pasquo and Martin 2013; Caramés *et al*. 2016) and, particularly, from the Late Cretaceous palynofloras of Cape Lamb, Vega Island (Askin 1988; Pirrie *et al*. 1991; Smith 1992) and The Naze, James Ross Island (Askin 1988).

Dettmann *et al*. (1990) hypothesized about the existence of an “Ancestral Group” of *Nothofagus* pollen comprising the earliest species in the pollen record (*Nothofagidites kaitangataensis*, *N. endurus,* and *N. senectus*), from which modern groups of pollen (*Nothofagus brassii*-, *fusca*-, and *menziesii*-type pollen) could have derived. No living species of *Nothofagus* produce pollen comparable to the ancestral ones although they share some characters with the living *fusca*- and *brassii*- groups. Dettmann *et al*. (1990) also suggested that Antarctica could

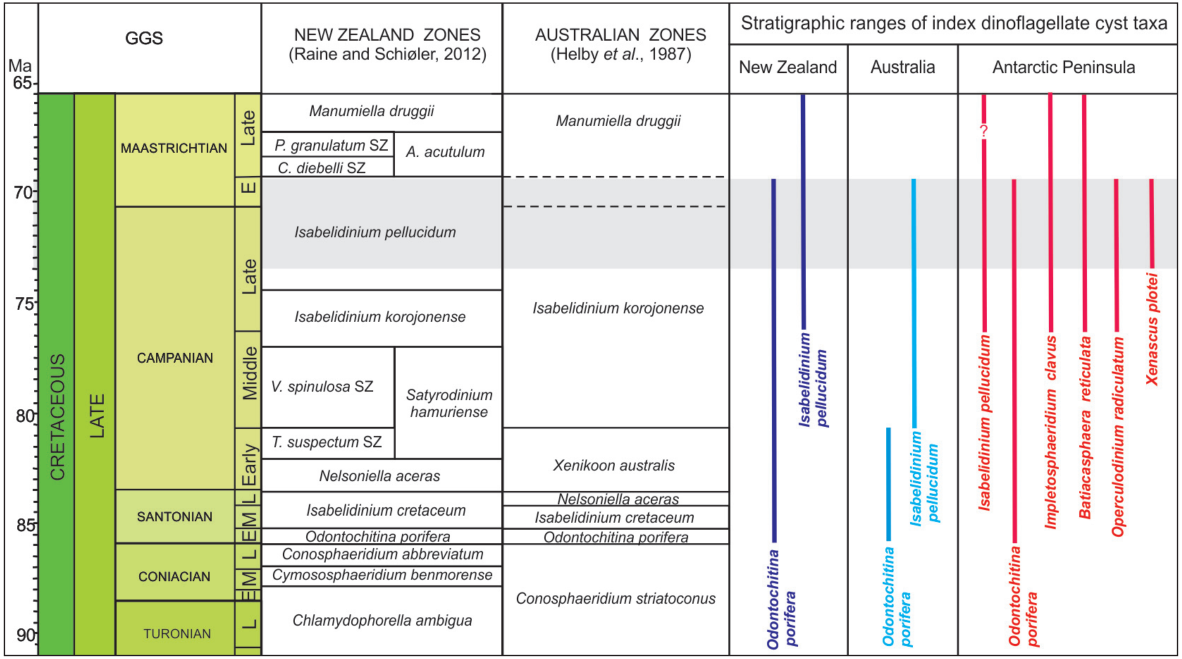

Fig. 4. Biostratigraphic zonation schemes and selected taxon ranges for New Zealand (after Raine and Schiøler 2012), Australia (after Helby *et al.* 1987) and Antarctic Peninsula (after Askin 1988; Dolding 1992; Smith 1992; di Pasquo and Martin 2003; Caramés *et al.* 2016). Grey area indicates the probable age for samples V2 and V6.

have been a diversification centre of *Nothofagus* during the Late Cretaceous (Campanian). Our report of the simultaneous presence in western Antarctica of two members of the "Ancestral Group", together with earliest records of pollen grains of the *Nothofagus brassii* -type would support the hypotheses proposed by Dettmann *et al*. (1990).

Dinoflagellate cysts were recorded in both samples of the section V2 and the biostratigraphic range of index species was taken into account as an age control of the fossil leaves studied herein. The Fig. 4 shows the biozonation of New Zealand and Australia based on dinoflagellate cyst and the stratigraphic ranges of index taxa of New Zealand, Australia, and the Antarctic Peninsula. Both samples of Section V2 have the same index dinoflagellate taxa; therefore both samples are considered closely similar in age. Based on the co-occurrence of *Isabelidinium pellucidum* (Deflandre and Cookson 1955) Lentin and Williams 1977, *Operculodinium radiculatum* Smith 1992, *Batiacasphaera reticulata* (Davey 1969) Davey 1979, and *Odontochitina porifera* Cookson 1956, the assemblages recovered from section V2 suggest a late Campanian to early Maastrichtian.

Most of the terrestrially-derived palynoflora comprises long-ranging taxa of limited stratigraphical value, spanning the Late Cretaceous and Paleocene of the Southern Hemisphere (Raine *et al*. 2011). Nevertheless, some taxa deserve to be taken into consideration. *Nothofagidites senectus*, recorded in samples of V2, may indicate an early Campanian and middle to early Maastrichtian age in terms of the Australian biozonation, because the species is a conspicuous element in both *Nothofagidites senectus* Zone (early Campanian) and the overlying *Tricolporites lilliei* Zone (middle Campanian-early Maastrichtian) in Australia (Helby *et al*. 1987); and is the most abundant *Nothofagidites* species in the *Nothofagidites senectus* Zone. In New Zealand, the first occurrence of *Nothofagidites senectus* defines the base of the PM1b Subzone (early-middle Campanian). This subzone is characterized by the association of *Forcipites sabulosus* and *Nothofagidites senectus* (Raine and Schiøler 2012). Considering both biozonal schemes, and in spite of the diachronism between the stratigraphic ranges of the Australian, New Zealand and Antarctic species, the assemblage here studied seems to fit better within the Australian biozonation suggesting Section V2 is within the early Campanian to early Maastrichtian interval. Previous studies indicate for the Snow Hill Island Formation a late Campanian – early Maastrichtian.

In the sample of section V6, palynomorph species have limited stratigraphical value due to their long ranges that span the Late Cretaceous and Paleocene (Raine *et al*. 2011).

Paleoenvironment and paleoclimate. — Pollen evidence suggests that during the middle Campanian – early Maastrichtian the continental landscape consisted of forests dominated by conifers and angiosperms, with *Nothofagus* as the main component, and rare cryptogams. This assumption agrees with

Poole and Cantrill's (2006) interpretation, who pointed out that Nothofagaceae was an important and diverse element of the Antarctic ecosystem (recorded by leaves, wood and pollen grains) in the middle Campanian. In the Maastrichtian, angiosperms continued increasing in abundance and diversity, evidenced by the appearance of other angiospermous taxa and the diversification of Nothofagaceae, while the conifers remained an important component of the vegetation. The paleoflora (mega and micro) of both Late Cretaceous units of Vega Island is suggesting the presence of a mixed coniferous and angiosperm forest with fern, and sporadic lycopods and moss understory.

The presence of marine palynomorphs in V2 and V6 indicated that both sections were deposited in nearshore environments, probably marginal ones due to the large amount of terrestrial palynomophs. The small dinoflagellate cyst *Impletosphaeridium clavus* (Wrenn and Hart 1988) emend. Bowman *et al*. 2013, which is present in both sections, is a conspicuous element in terms of abundance in Section V2 (in BAFC-Pl 1629 and 1630) while in section V6 only rare specimens were identified.

Warny *et al*. (2007) compared specimens of *Impletosphaeridium* recovered from Eocene to Miocene Antarctic deposits with modern dinoflagellate cysts species as potential modern analogues. They found morphological similarities between the fossils and the extant species. They considered that, as the extant species have a strong relationship with temporary sea-ice cover, the presence of *Impletosphaeridium* in Cenozoic Antarctic deposits could indicate the development of ephemeral sea-ice in the areas where these dinoflagellate cysts were abundant. Later, Bowman *et al*. (2013) suggested that the periodic profusion of *I. clavus* in the Maastrichtian of Seymour Island may be related to winter sea-ice formation and decay.

Additionally, Amenábar *et al*. (2014) demonstrated that although the gross morphology of *Impletosphaeridium* resembles modern species, they exhibit some morphological differences which prevent a confident comparison of the ecological requirements between fossil and modern species. Moreover, these authors suggested that the nutrient availability and physico-chemical properties of the water should be also considered as possible factors influencing the temporary profusion of *I. clavus* cysts. Finally, Amenábar *et al*. (2014) noted that the Late Cretaceous *Impletosphaeridium* acme recorded in high latitudes could be a combination of cold waters (but not necessarily sea-ice conditions) and a marine environment with nutrient-rich surface waters that would have favoured the dinoflagellate blooms.

The sedimentological data suggests that the lower CL Mb of the López de Bertodano Formation was deposited in an upward-shallowing, mid- to outer-shelf setting, although Olivero (2012) more precisely interpreted it as a progradational deltaic wedge. Moreover, the almost complete leaf and the slightly fragmented one, but with well-preserved details (high order venation), suggest they have undergone relatively little transport. The close proximity to the original vegetation is also supported by the dominance of terrestrially-derived palynomorphs over marine dinoflagellate cyst taxa. A nearshore environment with a high terrestrial input is evident. In this scenario characterized by nutrient-rich or eutrophic surface waters, the abundance of *Impletosphaeridium* may have occurred.

The sample from Section V6 from SB Mb of the López de Bertodano Formation, is characterized by gymnosperm pollen grains and scarce angiosperms, with notably only one species of *Nothofagidites* (*N. dorotensis*) and cryptogam spores. The fungi and the plant tissues are the common elements of the assemblage. The dominance of terrestrial palynomorphs and scarcity of marine forms suggest a nearshore shallow and marginal environment that is coincident with the increasing of terrestrial vertebrate fossil remains and nearshore taxa and increasing amounts of carbonaceous plant hash upwards in the SB Mb. This is consistent with culmination of shallowing within the basin, as proposed by Roberts *et al*. (2014), among others.

Fungal elements and especially the presence of Microthyriaceous fruiting bodies (Fig. 3W) in section V6 indicates a humid and temperate climate characterized by high relative ambient moisture (*e.g*., García Massini *et al*. 2004) for the vegetation that developed during the deposition of sample BAFC-Pl1486. Moist conditions probably prevailed in this part of the James Ross Island Basin and the moisture could have fostered the growth of fungi for example, within the woody debris that covered the forest floor during the Maastrichtian (Poole and Cantrill 2006).

Conclusions

1. The well-preserved material studied here allows detailed description of two leaves related to *Nothofagus*: *Nothofagus* sp. 1 from the lower CL Mb of Snow Hill Island Formation and Morphotype LDB 1 from the SB Mb. of López de Bertodano Formation, Cape Lamb, Vega Island, EAP. *Nothofagus* sp. 1 belongs to an ancestral, extinct group, with affinities to living species of the subgenera *Lophozonia* and *Fuscospora*.
2. The palynological assemblages obtained from the same levels or close to the fossil leaves allow us to suggest possible association of *Nothofagus* sp. 1 and Morphotype LDB 1 with the four species of *Nothofagidites* found (*N. senectus, N. kaitangataensis, N dorotensis,* and *Nothofagus* sp. *brassii*-type). Their presence supports the hypothesis that the diversification of the genus *Nothofagus* was well under way by the Campanian-Maastrichtian, as already pointed in previous reports. The two former species belong to an ancestral, extinct group, and the rest have affinities with living and fossil

species of the *brassii*-type of pollen, grouped mainly in the Subgenus *Brassospora*. Marine palynomorphs, especially dinoflagellate cysts agree with the age of the fossil leaves of Section V2 as late Campanian to early Maastrichtian based on the maximum range concurrence of the species. The pollen grain *Nothofagidites senectus* in Section V2 suggests an early Campanian to early Maastrichtian in terms of the Australian biozonal scheme. Section V6 has non-diagnostic taxa so it was not possible to refine the age beyond that provided by previous publications.

3. The presence of marine palynomorphs in Section V2 and V6 indicates a marginal marine depositional environment. Section V2 (CL Mb) represents a fully and marginal (because the high abundance of *I. clavus*) shallow marine paleoenvironment, with abundant invertebrates and rare terrestrial vertebrates, while Section V6 (SB Mb), shows a nearshore marine to possibly terrestrial, upward coarsening siliciclastic succession reflecting the culmination of shallowing within the basin. The result of the analyses of palynological assemblages supports the more nearshore environment for the López de Bertodano Formation than the underlying Snow Hill Island Formation. Pollen and spore evidence from Section V2 suggests nearby continental and forested areas dominated by conifers and angiosperms, with *Nothofagus* as the main component, and rarely cryptogams. The scenario for Section V6 was similar, but with the dominance of gymnosperm pollen grains over angiosperms, and common fungi fruits and plant tissues. A warm temperate climate characterized by high relative moisture is suggested for Section V6 based on the presence of the frequent fungal fossils.

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