UNIVERSIDADE DE SÃO PAULO
INSTITUTO DE GEOCIÊNCIAS

**PALEOBIOGEOGRAFIA DOS BIVALVIA CENOZOICOS DA
ANTÁRTICA**

Fernanda Quaglio

Orientador: Prof. Dr. Marcello Guimarães Simões

TESE DE DOUTORAMENTO
Programa de Pós-Graduação em Geoquímica e Geotectônica

SÃO PAULO
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“Life and earth evolve together”

Léon Croizat, 1964

Resumo

Grandes mudanças climáticas ocorridas no final do Paleógeno afetaram profundamente a distribuição e evolução de faunas marinhas e terrestres das porções austrais do Hemisfério Sul. Evidências geoquímicas apontam para a ocorrência de um grande evento de esfriamento global concomitante à expansão dos mantos de gelo na Antártica, no limite Eoceno/Oligoceno, marcando a passagem *greenhouse-icehouse* no planeta. Tais eventos foram deflagrados pela queda na concentração de gás carbônico atmosférico durante uma fase de mudança na obliquidade da Terra. Simultaneamente, a Antártica se isolou geograficamente, pela separação da Austrália e da América do Sul. A nova configuração tectônica alterou os padrões de circulação marinha e atmosférica nas altas latitudes, culminando na formação da Corrente Circum-Antártica.

Sob este aspecto, os bivalves representam um grupo adequado para estudos paleobiogeográficos, devido ao grande potencial de preservação e às características ecológicas, que auxiliam no entendimento da resposta biótica frente às mudanças ambientais e dinâmica das correntes marinhas ocorridas nas altas latitudes ao longo do Cenozoico.

A presente tese introduz novos dados a respeito dos depósitos relacionados aos principais eventos cenozoicos de glaciação antártica, como as formações Polonez Cove (Oligoceno inicial) e Melville (Mioceno inicial), na Ilha Rei George. Além disso, avalia, do ponto de vista paleobiogeográfico, a distribuição do registro de moluscos bivalves ao longo do Cenozoico nas porções austrais do Hemisfério Sul.

A descrição taxonômica de cinco novos registros, incluindo três espécies novas, contribui para o conhecimento da diversidade cenozoica de moluscos bivalves da Antártica. As análises paleobiogeográficas aplicaram, de forma inédita, métodos analíticos de biogeografia, como as análises de cluster e de parcimônia de endemidade e panbiogeografia, a partir de extensa lista de dados de ocorrência de gêneros de bivalves, do registro atual e fóssil, totalizando aproximadamente 900 gêneros, distribuídos em mais de 41.000 registros austrais cenozoicos.

Os resultados da presente tese confirmam a influência do histórico de mudanças ambientais ocorridas na Antártica na fauna de bivalves marinhos austrais ao longo do Cenozoico. A análise multivariada e de parcimônia de todos os gêneros de bivalves registrados do Cretáceo ao Recente em regiões austrais indica que a Província Weddelliana se fragmentou ainda no final do Cretáceo, sendo que as novas províncias austrais se definiram ainda no Paleógeno. O registro dos gêneros de bivalves cenozoicos da Formação Cape Melville sugere que os eventos glaciais na Antártica extinguíram apenas os gêneros de águas rasas, devido à restrição de habitats costeiros e plataformais após o avanço da plataforma de gelo no Plio-Pleistoceno.

Abstract

Pronounced climatic changes at the end of Paleogene deeply affected the distribution and evolution of marine and terrestrial southern faunas. Geochemical evidences indicate the global occurrence of a major cooling event along with to the ice sheet expansion in Antarctica, in the Eocene/Oligocene boundary, marking the greenhouse-icehouse shift in the planet. Those events were triggered by the drop of the atmospheric carbon dioxide during a phase of changing in the Earth's obliquity. At the same time, Antarctica became geographically isolated, following the separation from Australia and South America. The newly achieved tectonic configuration had a great effect on the marine and atmospheric circulation of the high latitudes, resulting in the development of the Circum-Antarctic Current.

In this context, the bivalve molluscs are a good macrofossil model taxon in paleobiogeographic studies as they have a high preservational potential and particular ecological requirements which may help in the understanding of the biotic responses to the environmental changes as well as marine currents dynamics occurred in the high latitudes along the Cenozoic.

This thesis introduces new data on the deposits associated to the main Antarctic glacial events in the Cenozoic, as the Polonez Cove (early Oligocene) and Melville (early Miocene) formations. Moreover, it evaluates, in a paleobiogeographic perspective, the distribution of the Cenozoic record of bivalve molluscs in the southernmost South Hemisphere.

The taxonomic description of five new records, including three new species, contributes to the knowledge of Cenozoic diversity of Antarctic bivalves. Paleobiogeographic analyses employed, for the first time, analytical method of biogeography, such as cluster analysis, parsimony analysis of endemism and panbiogeography, by means of a broad data set of Recent and fossil bivalve genera, reaching *c.a.* 900 austral genera, distributed in more than 41,000 Cenozoic austral records. The obtained results endorse the influence of Cenozoic environmental changes of the high latitudes in the southern marine bivalves. The multivariate and parsimony analyses of all bivalve genera recorded from the Cretaceous to Recent in the southern regions indicate that the Weddellian Province broke apart as early as the end of Cretaceous, and the new southern provinces formed in the Paleogene. The Cenozoic records of bivalve genus from the Cape Melville Formation suggest that the Antarctic glacial events extinguished only shallow genera, due to the restriction of shallow and shelfal habitats following the advance of the Antarctic ice shelf in the Plio-Pleistocene.

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Espécies de bivalves fósseis provenientes de depósitos cretácicos e cenozoicos da Antártica.

Anexo 3

Artigo 1: QUAGLIO F, WARREN LV, ANELLI LE, SIMÕES MG, STRIKIS PC, GHILARDI RP, GAŹDZICKI A, TIOSSI AB, SANTOS PR & ROCHA-CAMPOS AC. Submetido. Shell beds from the Low Head Member (Polonez Cove Formation, Early Oligocene) at King George Island, West Antarctica: new insights on facies analysis, taphonomy and paleoenvironmental significance. *Antarctic Science*.

Anexo 4

Artigo 2: QUAGLIO F, WHITTLE RJ, GAŹDZICKI A & SIMÕES MG. 2010. A new fossil *Adamussium* (Bivalvia: Pectinidae) from Antarctica. *Polish Polar Research* **31**(4): 291-302.

Anexo 5

Artigo 3: WHITTLE RJ, QUAGLIO F & CRAME JA. Nuculidae (Bivalvia) in the Cape Melville Formation, King George Island, Antarctica, with an overview of the bivalve fauna. 2012. *Antarctic Science* **24**(6): 625-633.

Anexo 6

Artigo 4: QUAGLIO F, ANELLI LE, NIHEI S, WHITTLE RJ, GRIFFITHS H, LINSE K, SIMÕES MG & GAŹDZICKI A. *Em preparação*. Bivalves from the Cape Melville Formation (early Miocene, West Antarctica): new taxa and paleobiogeography.

Anexo 7

Artigo 5: QUAGLIO F, GRIFFITHS H, LINSE K, WHITTLE RJ, NIHEI S & SIMÕES MG. *Em preparação*. Broken apart and frozen out: the fate of the Cenozoic southern marine fauna.

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1. CONSIDERAÇÕES INICIAIS

1.1. Introdução

Intensas alterações ambientais ocorridas ao longo do Cenozoico nas regiões mais austrais do Hemisfério Sul (Anexo 1) afetaram o clima global de forma significativa a partir do final do Paleógeno. Evidências fundamentadas em isótopos de oxigênio apontam para a existência de um grande evento de esfriamento global (Zachos *et al.* 2001, Coxall & Pearson 2007, Liu *et al.* 2009), concomitante à expansão dos mantos de gelo na Antártica (Coxall *et al.* 2005), durante o limite Eoceno/Oligoceno (Lear *et al.* 2008). Essas variações nas condições climáticas representaram a transição cenozoica da fase interglacial denominada “estufa” (*greenhouse*) para a fase glacial do planeta, chamada “refrigeradora” (*icehouse*; Miller *et al.* 1991).

O agente deflagrador dessas alterações tem sido motivo de intenso debate na última década. O cenário mais tradicionalmente aceito coloca dois eventos tectônicos resultando no isolamento geográfico da Antártica: a separação entre a Antártica e a Austrália, no limite Eoceno/Oligoceno, e a separação entre a Antártica e a América do Sul, no Oligoceno final (Barker & Burrell 1977, Kennett 1977, Toggweiler & Bjornsson 1999, Nong *et al.* 2000, Exon *et al.* 2001, Barker 2001, Robert *et al.* 2001). O isolamento térmico seria consequência direta do isolamento geográfico, a partir de mudanças nos padrões de circulação marinha e atmosférica, induzidas pela nova configuração tectônica (Kennett 1977, Robert *et al.* 2001).

Outro cenário, mais recentemente proposto, tem recebido mais adeptos na última década. Este sugere que o declínio do gás carbônico atmosférico estaria diretamente ligado à expansão dos mantos de gelo antárticos, no final do Paleógeno (DeConto & Pollard 2003a, b, Coxall *et al.* 2005, Pearson *et al.* 2009). O esfriamento teria sido causado somente pela queda da concentração de gás carbônico, como consequência do soerguimento e erosão do sistema orogênico Himalaia-Tibet (Raymo & Ruddiman 1992, Garzione 2008), ou adicionalmente a uma fase de mudança na obliquidade da Terra (DeConto & Pollard 2003a, b).

As mudanças em decorrência do esfriamento e reorganização das correntes oceânicas nas altas latitudes ao longo do Cenozoico afetaram a evolução biótica da região (Bartek *et al.* 1992, Crame 1992, 1999, Exon *et al.* 2001). Algumas propostas sugerem que as glaciações ocorridas ao longo do Cenozoico causaram a fragmentação de extensas províncias marinhas biogeográficas que existiram nas altas latitudes durante o Mesozoico e

boa parte do Neógeno, e a consequente extinção de diversos grupos marinhos e terrestres ao longo do Cenozoico (Zinsmeister 1979a, b, Stilwell & Zinsmeister 1992, Beu 2009). Entretanto, dados taxonômicos mais recentes e novos resultados de análises paleobiogeográficas, como os apresentados nesta tese, alteram ligeiramente esse cenário. Além de introduzirem novas informações sobre a diversidade pretéritas de moluscos antárticos, os novos estudos sugerem idades distintas para as principais mudanças no padrão de distribuição das faunas marinhas do que anteriormente proposto.

1.2. Justificativas e objetivos

Os moluscos bivalves possuem grande potencial em estudos de dinâmica de distribuição geográfica. Tratam-se de um dos grupos de macroinvertebrados mais diversificados e globalmente distribuídos ao longo do Fanerozoico, com história evolutiva relacionada a habitats bastante diversos. Além disso, durante o estágio pelágico de larva, os bivalves são capazes de migrar por longas distâncias por correntes oceânicas (Scheltema 1977), colonizando novos ambientes, como por exemplo, aqueles originados após eventos de abertura de passagens oceânicas. Sob esse aspecto, formam um grupo que potencialmente fornece informações importantes para o estudo do histórico climático e oceanográfico da Antártica (Belanger *et al.* 2012) sob o enfoque da paleobiogeografia.

Frente a esse panorama, esta tese está fundamentada na hipótese de que as mudanças ambientais ocorridas no sul do Hemisfério Sul durante o Cenozoico afetaram a distribuição dos organismos marinhos da Antártica, e possui os seguintes objetivos:

- Estudar taxonomicamente alguns dos bivalves de depósitos cenozoicos da ilha Rei George, Antártica, ainda não descritos;
- Acessar as bases de dados disponíveis para o levantamento de gêneros de bivalves registrados em depósitos cenozoicos de regiões austrais;
- Atualizar os dados obtidos, a partir da lista estabelecida previamente (Quaglio 2007);
- Tratar os dados de registro com métodos analíticos de biogeografia histórica;
- Interpretar os resultados de distribuição paleobiogeográfica e confrontá-los com estudo de distribuição biogeográfica da região antártica;
- Reavaliar hipóteses e conceitos de estudos paleobiogeográficos realizados com dados de moluscos dessa região.

2. CONTEXTO HISTÓRICO REGIONAL

2.1. O registro glacial

Os estudos sobre os vários aspectos relacionados ao histórico ambiental cenozoico da Antártica, tais como clima, biota, geologia, dinâmica de circulação oceânica e atmosférica, buscam de forma crucial o entendimento de como ocorreu a principal mudança climática global ocorrida nos últimos 50Ma. Muito embora o conhecimento acumulado nos últimos 50 anos tenha alcançado um panorama geral da evolução ambiental da Antártica, há ainda muitas controvérsias permeando o histórico cenozoico do continente em seus diversos aspectos. Isto, em parte, deve-se à dificuldade de acesso e demanda logística de exploração ao extenso território (cerca de 14 milhões de km²) e, portanto, à natureza fragmentária e enviesada das pesquisas científicas até hoje realizadas. Aproximadamente 98% do continente estão cobertos por gelo (Birkenmajer 2001), de tal sorte que apenas uma pequena porção do registro geológico está acessível para pesquisa e em poucas ocorrências no continente. Os dados geológicos comumente são obtidos nas porções costeiras, em áreas permanentemente ou sazonalmente desprovidas de cobertura de gelo, ou ainda por meio de testemunhagem.

Os dados de registro glacial da porção oriental da Antártica são provenientes principalmente de testemunhos coletados na região do Mar de Ross (Anexo 1) e Baía Prydz, como parte dos projetos de sondagem ODP (*Ocean Drilling Program*) e CIROS (*Cenozoic Investigations of the Ross Sea*). Os estudos com base nos dados provenientes desses testemunhos são geralmente de cunho sedimentológico e geoquímico, uma vez que não ocorrem afloramentos de idade paleógena nessas regiões.

Na porção ocidental da antártica, por outro lado, o registro glacial encontra-se exposto em diversas localidades da região peninsular. De forma generalizada, na Península Antártica encontra-se o registro geológico mais completo do Cenozoico da Antártica, sobretudo nas ilhas James Ross, Seymour, Cockburn e Rei George (Anexo 1A-B), em afloramentos extensos e representativos em área se comparados ao restante do continente.

2.1.1. Antártica Oriental

As idades atribuídas à presença de mantos de gelo nas regiões próximas à Baía Prydz e Platô de Kerguelen (Anexo 1A) correspondem ao final do Eoceno e início do

Oligoceno (Zachos *et al.* 1992, Cooper & O'Brien 2004). De fato, Barron *et al.* (1991) e Zachos *et al.* (1992) concluíram que o manto de gelo nessas regiões já alcançara volume semelhante ao atual ainda no início do Oligoceno. Bo *et al.* (2009) realizaram estudo a partir de dados de radar obtidos durante os verões de 2004 e 2007 em uma das localidades mais topograficamente elevadas da Antártica à época do esfriamento, as montanhas Gamburstev (Anexo 1A). Segundo os autores, essa região, provavelmente já glaciada antes do esfriamento em larga escala, foi o ponto de partida da expansão do manto de gelo antártico. Além disso, o evento de glaciação teria se iniciado por volta de 34Ma e perdurado pelos 20 milhões de anos seguintes. Essa interpretação corrobora os estudos de Barron *et al.* (1991) e Dingle & Lavelle (1998a), os quais afirmam que a glaciação da porção ocidental da Antártica teria se iniciado na região da Baía Prydz, localidade próxima às montanhas Gamburstev.

Já na região do Mar de Ross (Anexo 1A, F-G), estudos de sismoestratigrafia e geoquímica a partir de foraminíferos sugerem que a presença de geleiras na porção pacífica da Antártica oriental ocorreu somente a partir do final do Oligoceno (Leckie & Webb 1983, Zachos *et al.* 2001, Sorlien *et al.* 2007).

2.2. Antártica Ocidental

Os principais trabalhos geológicos e paleontológicos na nas ilhas da Península Antártica foram realizados na segunda metade da década de 1970 pelas expedições antárticas polonesas (Birkenmajer 2001). A partir do princípio da década de 80, foram publicados diversos estudos sobre estratigrafia, idade, paleogeografia e paleontologia (*e.g.* Birkenmajer 1982a, b, 1984, 1994, 1995, 1996, 2001, 2003, Birkenmajer *et al.* 1987a, b, Porebski & Gradzinski 1987, Troedson & Riding 2002, Troedson & Smellie 2002).

O registro de glaciação mais antigo na porção ocidental da Antártica está representado por um tilito de alojamento de 65m de espessura, localizado entre Hervé Cove e Breccia Crag, na Baía do Almirantado, Ilha Rei George (Birkenmajer *et al.* 2005) (Anexo 1C). Datado da metade do Eoceno, o depósito é interpretado como geleira de altitude, e não é considerado, portanto, como parte da glaciação em larga escala responsável pela expansão dos mantos de gelo na porção ocidental da Antártica (Birkenmajer *et al.* 2005).

Outras rochas cenozoicas presentes na Península Antártica, porém, parecem estar mais intimamente relacionadas à glaciação perene nessa região do continente. Segundo Birkenmajer (1991, 1996), os depósitos da Ilha Rei George representam quatro eventos de

glaciação ao longo de 30 Ma, do Eoceno (50 Ma) ao início do Mioceno (20 Ma), denominadas Krakow, Polonez, Legru e Melville. No entanto, Barker & Camerlenghi (2002) e Troedson & Smellie (2002) reconheceram apenas as glaciações Polonez e Melville como glaciações em larga escala, sendo a glaciação Krakow parte da Polonez, e a Legru considerada como um provável evento de glaciação local ou de altitude (Figura 1).

Glaciação Krakow

A glaciação Krakow seria representada por diamictitos fossilíferos aflorando em Magda Nunatak (Figura 1D-46), preservando bivalves, escafópodes e cocólitos, sobrepostos por brechas e fluxos de lava (Birkenmajer 1991, 1996).

Lavas basálticas de porções superiores da unidade foram datadas de 49,5 Ma pelo método de K-Ar (Eoceno inicial), enquanto estudos com nanoplâncton em sedimentos marinhos sugeriram Eoceno inicial a final (Birkenmajer 1991, 1996, Birkenmajer *et al.* 1986). No entanto, datações pelo método da razão Sr^{87}/Sr^{86} em conchas de braquiópodes e bivalves coletados nos depósitos de tilitos de Magda Nunatak forneceram idade de 29,8Ma (fim do Oligoceno inicial, de acordo com Dingle & Lavelle 1998b), o que torna tais depósitos correlatos a rochas mais tardias (da glaciação Polonez), invalidando a glaciação Krakow como evento isolado. De fato, Troedson & Smellie (2002) reconheceram os depósitos aflorantes em Magda Nunatak como pertencentes ao Membro Krakowiak Glacier da Formação Polonez Cove (Figura 1).

Glaciação Polonez

A glaciação Polonez é considerada a maior glaciação cenozoica da ilha (Birkenmajer 1991, 1996, 2001) e o primeiro evento de glaciação no oeste da Antártica (Dingle & Lavelle 1998a,b). Está representada pelos depósitos de diamictitos, conglomerados e arenitos fossilíferos da Formação Polonez Cove, que se estendem desde a Península de Low Head até a Península de Lions Rump, em Three Sisters Point, Penhasco Goodwin e Pico Vauréal (Birkenmajer 2001, Troedson & Smellie 2002, Quaglio *et al.* 2008) (Anexo 1D).

Datações nas rochas da Formação Polonez Cove indicaram idade entre 74-34 Ma (final do Cretáceo a Eoceno/Oligoceno) pelo método K-Ar (Birkenmajer *et al.* 1986), e 29,4 Ma (fim do Oligoceno inicial, Rupeliano) pelo método da razão Sr^{87}/Sr^{86} em conchas de bivalves (Dingle *et al.* 1997) (Figura 1).

Figura 1: O registro glacial da ilha Rei George. **A**, unidades litoestratigráficas cenozóicas da ilha Rei George. **B**, distribuição de depósitos glaciogênicos cenozóicos da Ilha Rei George (baseado em Birkenmajer 2001, Troedson & Riding 2002 e Barker & Camerlenghi 2002). **BP**, Formação Boy Point; **DB**, Formação Destruction Bay; **DR**, Formação Dunikowski Ridge; **HH**, Formação Harnasie Hill; **MH**, Formação Martins Head; **SB**, Formação Sherrat Bay; **VP**, Formação Vauréal Peak.

a, datação por K-Ar de lavas basálticas de Polonez Cove (Birkenmajer & Gaździcki 1986).
b, datação por K-Ar de lavas andesíticas de Turret Point (Birkenmajer *et al.* 1989).
c, datação por K-Ar de lavas andesíticas de Lions Rump (Smellie *et al.* 1984).
d, datação por $^{87}\text{Sr}/^{86}\text{Sr}$ em conchas de bivalves de tilitos do Membro Krakowiak Glacier Member em Polonez Cove (Dingle & Lavelle 1998b).
e, datação por $^{87}\text{Sr}/^{86}\text{Sr}$ em conchas de bivalves de conglomerados do Membro Low Head em Low Head, Polonez Cove e Lions Rump (Dingle *et al.* 1997).
f, datação por $^{87}\text{Sr}/^{86}\text{Sr}$ em conchas de bivalves e braquiópodes de tilitos basais em Magda Nunatak (Dingle & Lavelle 1998b).
g, idade mínima obtida por K-Ar de lavas andesíticas e dacíticas de Polonez Cove e Boy Point (Birkenmajer & Gaździcki 1986).
h, datação por K-Ar de lavas andesíticas provenientes de Dunikowski Ridge (Birkenmajer 2001).
i, datação por K-Ar de lavas andesíticas em Martins Head (Birkenmajer *et al.* 1989).
j, datação por K-Ar de lavas andesíticas do topo da Formação Martins Head (Birkenmajer *et al.* 1986).
k, datação por $^{87}\text{Sr}/^{86}\text{Sr}$ em conchas de braquiópodes em Wrona Buttress (Dingle & Lavelle 1998b).
l, datação por $^{87}\text{Sr}/^{86}\text{Sr}$ em conchas de braquiópodes (Dingle & Lavelle 1998b).
m, datação por K-Ar de tufas na base da formação (Birkenmajer *et al.* 1988).
n, datação por $^{87}\text{Sr}/^{86}\text{Sr}$ em conchas de bivalves (Dingle & Lavelle 1998b).
o, datação por K-Ar de diques andesíticos que cortam a formação (Birkenmajer *et al.* 1985).
p, Glaciações segundo Birkenmajer (2001), Troedson & Riding (2002) e Barker & Camerlenghi (2002).

O Membro Krakowiak Glacier dessa formação é caracterizado por fácies de conglomerados e diamictitos, contendo clastos facetados e estriados, de origem alóctone, a partir das Montanhas Transantárticas e Ellsworth (Birkenmajer 1996, 2001, Troedson & Smellie 2002, Quaglio *et al.* 2008) (Anexo 1A). Tais características representam evidência da presença pretérita de mantos de gelo, que teriam transportado fragmentos líticos da região central para a extremidade ocidental da Antártica (Birkenmajer 1996, 2001, Troedson & Smellie 2002). Este fenômeno corrobora a existência de glaciação perene nesta região, no início da deposição da Formação Polonez Cove (Birkenmajer 1996, 2001, Troedson & Smellie 2002). Além disso, conchas de braquiópodes coletadas do Membro Low Head da Formação Polonez Cove sugeriram paleotemperaturas de 3° - 3,8°C (Quaglio & Santos 2006). Portanto, os dados sedimentológicos e isotópicos corroboraram a hipótese de que a glaciação Polonez representa o primeiro evento cenozoico de glaciação em larga escala no oeste da Antártica, embora com temperaturas mais amenas que as atuais (Tripathi *et al.* 2005).

Glaciação Legru

A glaciação Legru teria ocorrido entre as glaciações Polonez e Melville (Birkenmajer 1980, 1983) e estaria representada por tilitos, andesitos e fluxos de detritos do tipo *lahar* da Formação Vauréal Peak (Figura 1), presentes nas proximidades da baía do Almirantado (Birkenmajer 1982a, 2001) (Anexo 1C). Birkenmajer *et al.* (1986), com base na datação das rochas da Formação Vauréal Peak pelo método do K-Ar, atribuíram à glaciação Legru idade de Oligoceno inicial (30-26 Ma), corroborada pelo método da razão Sr^{87}/Sr^{86} por Dingle *et al.* (1997) (Figura 1).

No entanto, Barker & Camerlenghi (2002), com base em discussões pessoais com J. Smellie, consideraram este evento como a glaciação mais jovem da ilha, embora de idade indefinida. Por outro lado, P.R. Santos (comunicação verbal, 2008) ponderou que a glaciação Legru é caracterizada como um evento local de altitude, típico de montanhas, e, portanto, deve ser excluído do evento regional de glaciação em larga escala – a glaciação Polonez - ocorrido no oeste da Antártica.

Glaciação Melville

O intervalo glacial mais jovem, denominado glaciação Melville, está representado por depósitos glaciomarinheiros fossilíferos da Formação Cape Melville, aflorantes em toda a extensão da Península Melville (Birkenmajer 1982b, Troedson & Riding 2002) (Anexo 1C).

A datação por K-Ar dos diques andesíticos e basálticos sugere idades de 20-23 Ma (início do Mioceno) (Birkenmajer 1985, 1988, Birkenmajer *et al.* 1988), a qual é corroborada por foraminíferos (Birkenmajer & Luczkowska 1987) e palinomorfos (Troedson & Riding 2002), provenientes da Formação Cape Melville (Figura 1).

As glaciações da ilha Rei George e os mantos de gelo do oeste

Zachos *et al.* (1994, 2001), com base no registro isotópico de oxigênio, consideraram que os mantos de gelo teriam se desenvolvido no leste da Antártica no início do Oligoceno, e alcançado o oeste durante o Mioceno médio. No entanto, Dingle & Lavelle (1998a) consideraram que o primeiro evento de glaciação perene no oeste da Antártica teria ocorrido já no final do Oligoceno inicial (29,8 Ma) e, posteriormente, um segundo pico de glaciação teria ocorrido no início do Mioceno (22,6 Ma). De fato, Barker & Camerlenghi (2002) afirmaram que, neste último intervalo de tempo, os mantos de gelo cobriam virtualmente todo o continente, estendendo-se, inclusive, na sua porção ocidental. É possível, portanto, que a glaciação miocênica apontada por Zachos *et al.* (1994, 2001) corresponda ao segundo evento de Dingle & Lavelle (1998a).

Considerando os eventos globais de incursão negativa da curva isotópica de oxigênio (Zachos *et al.* 1994, 2001) e as idades atribuídas às formações Polonez Cove (Birkenmajer *et al.* 1986, Dingle *et al.* 1997) e Cape Melville (Birkenmajer *et al.* 1988, Troedson & Riding 2002, Birkenmajer & Luczkowska 1987), o primeiro e segundo eventos que configuraram a glaciação em larga escala no oeste do continente correspondem, respectivamente, às glaciações Polonez, quando foram depositados os sedimentos da Formação Polonez Cove, e Melville, quando foi depositada a Formação Cape Melville (Figura 1B).

2.2. Paleogeografia da Antártica

Atualmente, a Antártica é circundada por seis placas organizadas em cristas de espalhamento tectônico (Torsvik *et al.* 2008; Figura 2). O continente é composto por duas províncias geológicas com histórias tectônicas distintas: a porção cratônica, formada pela Antártica Oriental, e a porção formada por diversos blocos tectônicos separados por riftes e depressões topográficas, compondo a Antártica Ocidental. A porção cratônica compreende terrenos amalgamados durante o Neoproterozoico, que formavam, juntamente com o sudoeste da Austrália, a porção centro-norte e noroeste do supercontinente Rodínia (Torsvik *et al.* 2008, Reguero *et al.* 2013). Dados paleomagnéticos sugerem que a porção oriental teria migrado paulatinamente de latitudes mais baixas desde

o Neoproterozoico até altas latitudes durante o Jurássico, quando teria alcançado, após a ruptura da Pangeia, posição próxima à atual (Torsvik & Van der Voo 2002). Sob este cenário, a Antártica teria experimentado condições tropicais durante o pré-Cambriano, passando para condições tropicais a subtropicais entre o final do Neoproterozoico e início do Paleozoico, posteriormente teria migrado para latitudes de clima temperado e polar durante o Paleozoico e boa parte do Mesozoico, e alcançado latitudes polares a partir de então (Torsvik *et al.* 2008).

Figura 2: Fisiografia atual e idades do fundo oceânico em torno da Antártica em milhões de anos (Ma). Setas brancas representam direção do movimento fundamental em reconstituição de hotspots dos últimos 5Ma. Círculos vermelhos indicam localização dos hotspots (BH, Bouvet; KH, Kerguelen; MH, Marion; RH, Reunion; SH, St. Helena; TH, Tristan). Grandes províncias ígneas e outras províncias vulcânicas indicadas em marrom e branco. Limites ativos de placa indicados em preto (cristas meso-oceânicas) e extintos em cinza. (extraído de Torsvik *et al.* 2008, fig. 2).

A porção ocidental da Antártica surge no registro geológico durante uma longa fase acrescionária que teve início no final do Neoproterozoico, a qual originou também as porções do leste da Austrália e oeste da América do Sul (Reguero *et al.* 2013).

Durante boa parte do Mesozoico, o continente Gondwana formava uma massa terrestre contínua ao longo da margem sul do Oceano Pacífico (Hay *et al.* 1999). A leste encontrava-se a região compreendida entre Austrália-Nova Guiné, Nova Zelândia e leste da Antártica. Já a oeste estava localizada a região de Marie Byrd Land, Península Antártica e o sul da América do Sul (Zinsmeister 1982) (Figura 3).

Figura 3: Paleogeografia da Antártica e regiões austrais no Cretáceo inicial (130Ma; modificado de Torsvik *et al.* 2008).

Na porção leste, grande parte dos mares rasos se aprofundou a partir do final do Cretáceo, restando apenas algumas bacias australianas (Zinsmeister 1987). Na região da Nova Zelândia, diversas áreas emersas resultantes de eventos de dobramento e soerguimento mantinham-se separadas do craton formado pela Antártica oriental (Bradshaw 1991, Larter *et al.* 2002).

A porção oeste consistia de um arco magmático (sul da América do Sul e Península Antártica) localizado em uma zona de subducção ao longo da margem pacífica ocidental e de diversos blocos crustais conectando o arco ao craton (Storey 1991, Jokat *et al.* 1997) (Figura 3). No final do Mesozoico, esta região estava ocupada por um conjunto imbricado de pequenas ilhas montanhosas, cercadas por mares rasos, o que facilitava o intercâmbio biótico de organismos plantônicos por mares rasos entre a porção ocidental da Antártica e sul da América do Sul.

2.3. O esfriamento antártico

Muito embora a Antártica já estivesse suscetível a clima polar desde que alcançou o pólo Sul, há aproximadamente 120 Ma, no início do Cretáceo (DiVenere *et al.* 1994), o esfriamento intenso do continente ocorreu dezenas de milhões de anos mais tarde, durante o final do Paleógeno. Os motivos, no entanto, podem ser associados a diversos fatores, desde eventos tectônicos, fatores de retroalimentação (dinâmica de circulação de correntes marinhas e atmosféricas, efeitos do albedo) e alteração nos ciclos orbitais do planeta.

Tradicionalmente, aceitava-se que o isolamento térmico dependeu diretamente do seu isolamento geográfico (Barker & Thomas 2004), resultado dos eventos tectônicos de abertura das passagens da Tasmânia e de Drake, no Paleógeno (Barker & Burrell 1977, Toggweiler & Bjornsson 1999, Exon *et al.* 2001).

A Passagem da Tasmânia se desenvolveu a partir do riftamento entre a região oriental da Antártica e sul da Austrália, datada anteriormente do limite Eoceno/Oligoceno (Exon *et al.* 2001), idade próxima ao início da glaciação antártica (Lear *et al.* 2008). No entanto, estudos recentes demonstraram que a abertura da Passagem da Tasmânia teria ocorrido ainda durante a metade ou final do Eoceno (Huber *et al.* 2004), anterior, portanto, ao o início da glaciação.

As idades propostas para o início da abertura da Passagem de Drake variam entre o início do Oligoceno (28 a 30Ma, Toggweiler & Bjornsson 1999) até o Eoceno médio (41Ma, Scher & Martin 2006; 45Ma, Livermore *et al.* 2007). A Corrente Circum-Antártica teria se estabelecido no final do Oligoceno (*e.g.* 24 Ma, Livermore *et al.* 2004) ou mesmo no limite Eoceno-Oligoceno (34Ma, Scher & Martin 2006). Por outro lado, a presença de cristas no assoalho oceânico e fragmentos de crosta continental no Mar de Scotia teriam impedido a passagem das correntes até o início do Oligoceno, em torno de 30 Ma (Livermore *et al.* 2007), ou início do Mioceno, por volta de 20 a 22 Ma (Lear *et al.* 2000, Eagles & Livermore 2002, Livermore *et al.* 2007). No entanto, evidências com base na assinatura de isótopos de neodímio indicam a entrada de águas do setor Pacífico no setor Atlântico ainda no início do Eoceno (Scher & Martin 2006).

Com a formação da Corrente Circum-Antártica, parte boa parte do calor transportado para o continente antártico seria bloqueado, mantendo, portanto, a Antártica isolada termicamente das regiões periféricas (Kennett 1977, Toggweiler & Bjornsson 1999). Este cenário, no entanto, tem sido descartado. De fato, na última década, resultados provenientes de testemunhagem e modelagens de circulação atmosférica e oceânica

colocam a variação na concentração de gases de efeito estufa no papel principal para a mudança climática global e manutenção da glaciação em larga escala na Antártica.

No entanto, a discussão sobre o papel das aberturas oceânicas austrais parece ainda não ter se encerrado. Estudo recente fundamentado em simulações de circulação oceânica sugeriu que a abertura da Passagem de Drake, de fato, contribuiu para a glaciação antártica (Cristini *et al.* 2012). Os resultados foram obtidos sem a inclusão de parâmetros que poderiam interferir com a glaciação, como vegetação, topografia, queda da concentração de gás carbônico atmosférico e configuração orbital da Terra.

2.3.1. Declínio do gás carbônico atmosférico

DeConto & Pollard (2003a, b) realizaram estudo com base em modelagem incluindo diversas variáveis ambientais, alterando a concentração de gás carbono atmosférico segundo as variações nos parâmetros orbitais da Terra. O modelo sugere que o esfriamento antártico teria sido desencadeado após mudanças orbitais bruscas, que teriam gerado verões mais frios. Nessas condições, a queda da concentração do gás carbônico atmosférico teria deflagrado a expansão do gelo em um intervalo de tempo geológico relativamente curto. Neste cenário, o isolamento geográfico teria desempenhado papel secundário no histórico do esfriamento cenozoico do continente.

Pearson *et al.* (2009), com base em curvas de oxigênio isotópico disponíveis e análises de boro isotópico registrado em conchas de foraminíferos, concluíram que o lento declínio da temperatura de águas profundas foi concomitante ao declínio de cerca de 30% da concentração de gás carbônico atmosférico, durante a fase inicial de expansão dos mantos de gelo antárticos. Esse resultado confirma o modelo e as interpretações de DeConto & Pollard (2003a, b). Pagani *et al.* (2011) estimaram queda de cerca de 40% na concentração de CO₂ atmosférico durante o limite Eoceno-Oligoceno (~33,7Ma), sendo que os menores valores são encontrados cerca de 2Ma previamente à deflagração da glaciação. Esta tendência de queda persistiria ao longo de todo o Oligoceno, culminando em um Mioceno com baixas temperaturas, embora mais amenas do que as atuais.

Diversos eventos de oscilação da extensão de gelo teriam ocorrido no final do Paleógeno, com o gelo raramente atingindo a plataforma (Retallack *et al.* 2001). Somente a partir do Plio-Pleistoceno, por volta de 1Ma, o volume de gelo antártico teria se expandido e alcançado as áreas plataformais, como consequência da alteração nos padrões de insolação em resposta a mudanças orbitais (Raymo *et al.* 2006).

A curva de oxigênio isotópico mostra diversas incursões do início à metade do Eoceno (Zachos *et al.* 2001, 2005). As oscilações do início do Eoceno não seriam representativas de glaciações, apenas de quedas intermitentes de temperatura. Já as oscilações do final do Eoceno ao início do Oligoceno (evento Oi-1, de Zachos *et al.* 2001) acopladas às mudanças no ciclo orbital da Terra, teriam desencadeado mudanças intensas no regime geoquímico marinho, resultando na expansão e estabilização dos mantos de gelo da Antártica (Merico *et al.* 2008). O desequilíbrio entre o sequestro de carbonato de cálcio da plataforma e o oceano profundo teria sido causado após a redução da área de plataformas carbonáticas pela queda do nível do mar em resposta a glaciações localizadas. A diminuição do sequestro de carbonato de cálcio nas plataformas acrescida do aumento do intemperismo em áreas plataformais anteriormente submersas resultaria em excesso de carbonato nas regiões mais profundas. O efeito compensatório desse aumento de carbonato inorgânico teria sido o aumento da alcalinidade oceânica e de íons carbonato em regiões mais profundas. Como resultado, os limites de profundidade de compensação do carbonato de cálcio se alterariam em mais de 1km. Tal reação em cadeia explicaria a queda do gás carbônico atmosférico após a redução da profundidade de compensação de carbonato e pelo consequente aumento do sequestro de carbono oceânico.

2.4. Síntese do esfriamento

A Figura 4 sintetiza os principais eventos ocorridos na região antártica durante o Cenozoico. No início do Oligoceno, a queda abrupta na temperatura (Zachos *et al.* 2001) teria transformado o sistema climático do Oceano Austral extremamente sensível à formação e/ou expansão de geleiras na Antártica (DeConto & Pollard 2003a, b). No leste da Antártica, esta fase está registrada nos depósitos de fluxo de detritos glaciais da região da Baía Prydz (Barron *et al.* 1991), sendo possível que a expansão do gelo tenha se iniciado a partir de uma grande área onde a glaciação de altitude se fazia presente (Bo *et al.* 2009).

Neste intervalo de tempo, de acordo com o modelo proposto por DeConto & (Pollard 2003a, b), é possível que a concentração de gás carbônico atmosférico fosse de aproximadamente três vezes a concentração moderna. No entanto, os parâmetros orbitais do planeta favoreciam a existência de verões mais curtos, o que promovia a acumulação de neve de altitude em áreas mais extensas. Com a variação nos parâmetros de excentricidade da Terra, as áreas mais topograficamente elevadas do leste da Antártica já glaciadas

Figura 4: Diagrama sintetizando os principais eventos cenozoicos e fatores que levaram ao isolamento térmico da Antártica. As caixas (eventos) estão organizadas de acordo como tempo geológico, e as setas indicam a relação entre os eventos a partir do surgimento provável dos mesmos (Curva isotópica extraída de Zachos *et al.* 2001; diagrama a partir de Bartek *et al.* 1992, Pagani *et al.* 1999, Toggweiler & Bjornsson 1999, Nong *et al.* 2000, Pearson & Palmer 2000, Exon *et al.* 2001, Zachos *et al.* 2001, Barker & Camerlenghi 2002, DeConto & Pollard 2003 a, b, Livermore *et al.* 2004, 2007, Coxall *et al.* 2005, Pfuhl & McCave 2005, Tripartti *et al.* 2005, Lear *et al.* 2008, Scher & Martin 2006, Cristini *et al.* 2012.)

passaram a coalescer. Esse fenômeno teria se desenvolvido rapidamente após a abertura da Passagem da Tasmânia e aumento do aporte de umidade para o continente (Exon *et al.* 2001).

Com a queda paulatina da concentração de gás carbônico atmosférico, os mantos de gelo do leste se expandiram rapidamente, alcançando a porção oeste da Antártica no final do Oligoceno inicial. Esse evento está registrado nas rochas da Ilha Rei George (Membro Krakowiak Glacier da Formação Polonez Cove), durante a Glaciação Polonez (Birkenmajer 1991, 1996). Com isso, a expansão dos mantos de gelo antárticos teriam levado cerca de 4Ma desde o leste até chegar ao oeste do continente (Dingle & Lavelle 1998a).

Após esta fase, o crescimento dos mantos de gelo teria sofrido flutuações, representado pelo aumento de temperatura (Zachos *et al.* 2001), tendo se expandido na região do Mar de Ross (Sorlien *et al.* 2007), e retraído na Península Antártica (Birkenmajer 1991, 1996). Após essas oscilações do final do Oligoceno à metade do Mioceno, mudanças no padrão de insolação provocadas pela variação no ciclo de obliquidade da Terra teriam resultado no avanço das geleiras terrestres para as regiões plataformais na Antártica (Raymo *et al.* 2006).

Com as aberturas das passagens oceânicas e a circulação da Corrente Circum-Antártica, organismos plantônicos passaram a encontrar novas vias de migração nas altas latitudes. No entanto, aqueles de águas frias ou euritêrmicos poderiam, potencialmente, ocupar as novas condições dos ambientes polares. Este tema é abordado nos anexos 6 e 7 do presente documento, que tratam dos estudos de evolução da distribuição paleobiogeográfica Cenozoica dos moluscos bivalves austrais.

3. PALEONTOLOGIA

3.1. O registro fóssil de moluscos bivalves

No Oceano Austral, Austrália, Nova Zelândia e sul da América do Sul destacam-se como as regiões intimamente ligadas ao histórico do isolamento antártico (Anexo 1).

O registro paleontológico de bivalves da Nova Zelândia é, sem dúvida, o mais bem estudado da região, com os trabalhos extensos e atualizados de Beu & Maxwell (1990) e Beu & Raine (2009), que reúnem mais de uma centena de gêneros de bivalves registrados de depósitos cenozoicos.

A literatura taxonômica de bivalves cenozoicos da Austrália inclui lista relativamente extensa de táxons descritos desde a década de 1920 (Whitehouse 1925, Singleton 1941, 1943, Darragh 1965a, b, 1986, 1997, Ludbrook 1969, 1983, Beu 1985, Buonaiuto 1977, Kendrick 1977, Darragh & Kendrick 2000, Stilwell 2005). No entanto, não há trabalhos recentes de revisão de grupos mais inclusivos, tratando várias famílias. Destaca-se apenas a revisão de Beu & Darragh (2001) para os pectinídeos cenozoicos do sul da Austrália.

Já os trabalhos taxonômicos de bivalves fósseis coletados no sul da América do Sul, sobretudo na Patagônia argentina, iniciaram-se no final do século XIX (Ihering 1897, 1902, 1904, 1907, Cossmann 1899, Ortmann 1902). Posteriormente, diversas espécies identificadas nesses trabalhos pioneiros foram reestudadas e novas descritas, o que contribuiu para o conhecimento da diversidade cenozoica de moluscos bivalves dessa região (Camacho & Fernández 1956, Zinsmeister 1981, Morra 1985, Erdmann & Morra 1985, Morra & Erdmann 1986, Griffin 1990, Parma *et al.* 1990, del Río 1992, 1995, 1997, 2004, del Río & Camacho 1996, 1998, Martínez & del Río 2002, Griffin & Pastorino 2006, dentre outros). No entanto, diversos exemplares depositados em coleções argentinas ainda não foram estudados (Beu *et al.* 1997), enquanto outros constam apenas como registro, e carecem, portanto de reestudo taxonômico (del Río 2004).

O conhecimento atual sobre a diversidade cenozoica dos bivalves antárticos é relativamente baixo, se comparado com o das demais regiões do Oceano Austral (Quaglio *et al.* 2007a, b). Conforme destacado anteriormente, a dificuldade de acesso a um território quase completamente coberto por gelo reflete o conhecimento bastante fragmentado sobre a história pretérita do continente.

As melhores exposições registrando bivalves ocorrem no extremo norte da Península Antártica (Anexo 1A-E). Os bivalves são encontrados em depósitos datados do final do Cretáceo (Formação López de Bertodano, ilhas James Ross e Seymour), Paleoceno inicial (Formação Sobral, ilhas James Ross, Snow Hill, Seymour e Vega), Eoceno inicial a médio (Formação La

Meseta, Ilha Seymour), Oligoceno inicial e final (formações Polonez Cove e Destruction Bay, Ilha Rei George), Mioceno inicial (Formação Cape Melville, Ilha Rei George) e Plioceno inicial (Formação Cockburn Island, Ilha Cockburn) (Gaździcki & Pugaczewska 1984, Pugaczewska 1984, Zinsmeister 1984, Stilwell & Zinsmeister 1987, Zinsmeister & Macellari 1988, Studencka 1991, Stilwell *et al.* 2002, Jonkers 2003, Anelli *et al.* 2006, Quaglio *et al.* 2008, Whittle *et al.* 2011). Algumas localidades possuem registro fóssil que antecede (como a Ilha Seymour) ou sucede (como as ilhas Rei George e Cockburn) o esfriamento antártico, e são, portanto, importantes para o conhecimento paleobiogeográfico cenozoico do grupo.

As ilhas Seymour, James Ross, Snow Hill e Vega (Anexo 1B) compreendem a região atualmente conhecida mais rica em fósseis do Cretáceo e Cenozoico de toda a Antártica. Os depósitos das formações López de Bertodano (Cretáceo final), Sobral (Paleoceno) e La Meseta (Eoceno) registram fósseis de diversos grupos, dentre eles (a) ostrácodes (Szczechura 2001), (b) equinodermes (Blake & Aronson 1998), (c) artrópodes (Feldmann & Zinsmeister 1984, Feldmann *et al.* 2003), (d) anelídeos (Schweitzer *et al.* 2005), (e) peixes condríctios (Stahl & Chatterjee 2002), (f) pinguins (Jadwiszczak 2006), (g) plesiossauros (Fostowicz-Frelik & Gaździcki 2001) e (h) mamíferos terrestres (Reguero *et al.* 2002), além de icnofósseis de invertebrados (Uchman & Gaździcki 2006, Nelson *et al.* 2008).

Dentre os estudos taxonômicos sobre os bivalves registrados nos depósitos cenozoicos da ilha Seymour, Zinsmeister (1984) identificou 11 espécies e erigiu 22 novas espécies de bivalves da Formação La Meseta. Zinsmeister & Macellari (1988) descreveram 18 espécies e propuseram 15 novas espécies desse grupo das formações López de Bertodano (Cretáceo final) e Sobral (Paleoceno).

A Ilha Cockburn (Anexo 1B), próxima da ilha Seymour, tem fósseis registrados nas formações Snow Hill Island (Cretáceo final) e Cockburn Island (Plioceno final), além da Formação La Meseta. Da Formação Snow Hill Island, Stilwell & Zinsmeister (1987) descreveram oito espécies de bivalves. A partir do registro da Formação La Meseta, os mesmos autores descreveram seis espécies de bivalves. A sucessão sedimentar representada pela Formação Cockburn Island (Ilha Cockburn) é caracterizada pela presença de coquinas de pectinídeos (*Pecten conglomerate*), da qual foram descritas três espécies de bivalves (Jonkers 2003).

Os depósitos fossilíferos cenozoicos da Ilha Rei George (Anexo 1B, C-E) que preservam bivalves estão representados nas formações Polonez Cove (em Lions Rump, Pico Vauréal e em Magda Nunatak), Destruction Bay (em Wrona Buttress) e Cape Melville (na Península Melville).

Da Formação Polonez Cove, na região de Low Head (Anexo 1D), foram descritas 28 espécies de bivalves (Gaździcki & Pugaczewska 1984, Pugaczewska 1984), além de cocólitos, diatomáceas, foraminíferos, serpulídeos, briozoários, braquiópodes, gastrópodes, ostrácodes,

crinoides, ofiuroides e equinoides. A assembleia é proveniente da coquina de pectinídeos do Membro Low Head, na região de Lions Rump (Anexo 1D), área-tipo da Formação Polonez Cove. Nessa localidade, o Membro Low Head ocorre como espessos níveis coquinoides compostos por conglomerados bioclasto-suportados, formados por valvas desarticuladas e geralmente completas de pectinídeos (*Pecten conglomerate*), semelhantes às encontradas na Ilha Cockburn (Birkenmajer 2001). O estudo tafonômico dos níveis de coquinas da Formação Polonez Cove é abordado mais adiante nesta tese, estando detalhado no anexo 3.

Da mesma unidade aflorante na região de Vauréal Peak, distante cerca de 5km de Low Head (Anexo 1C, D), Quaglio *et al.* (2008) descreveram três espécies de bivalves, duas de braquiópodes, além de restos de briozoários, serpulídeos e equinodermes. Também da mesma formação e membro, aflorantes na região de Magda Nunatak (Anexo 1D), Pugaczewska (1984) descreveu três espécies de bivalves das famílias Veneridae e Hiatellidae.

Da Formação Destruction Bay, cujas exposições ocorrem nas proximidades da península Melville (Anexo 1C, E), Studencka (1991) descreveu duas espécies de bivalves da Família Hiatellidae. Uma nova espécie de pectinídeo proveniente desta unidade foi estudada na presente tese e será abordada no capítulo de Resultados e Anexo 4.

Da Formação Cape Melville, aflorante ao longo da Península Melville (Anexo 1C e E), foram descritos vários grupos taxonômicos, como braquiópodes (Biernat *et al.* 1985, Bitner & Crame 2002), crustáceos (Föster *et al.* 1987, Feldman & Crame 1998, Feldmann & Gaździcki 1997, 1998), equinoides (Jesioneck-Szymanska 1987), cefalópodes (Birkenmajer *et al.* 1987b), gastrópodes (Karczewski 1987), corais (Roniewicz & Morycowa 1987) e plantas (Birkenmajer & Zastawniak 1986). No entanto, a despeito de sua abundância relativa nesta formação (Birkenmajer 1982b, 1984, Birkenmajer *et al.* 1987b, Troedson & Riding 2002), até o presente haviam sido descritas sete espécies em seis gêneros de bivalves (Anelli *et al.* 2006). No contexto desta tese, o capítulo de Resultados e os anexos 5 e 6 tratam das novas descobertas taxonômicas da unidade, que incluem quatro novas espécies de bivalves.

Jonkers (2003) reestudou os quatro gêneros de pectinídeos provenientes de depósitos cenozoicos do Oceano Sul, abrangendo diversas localidades no sul da América do Sul, Antártica e ilhas próximas à zona da Convergência Antártica, Nova Zelândia e Tasmânia (Anexo 1A). O estudo compreendeu o total de 22 espécies, incluindo dois gêneros novos e quatro espécies novas, além da sinonimização de pectinídeos anteriormente descritos por Gaździcki & Pugaczewska (1984) e Stilwell *et al.* (2002).

Diferentemente de sua porção ocidental, a Antártica oriental possui áreas de afloramento mais raras e restritas, sobretudo aquelas onde conchas de bivalves estão preservadas. Embora menos abundantes em comparação com o registro fóssil da Península Antártica, os dados

paleontológicos provenientes de testemunhos de sondagens são importantes especialmente devido ao fato de que a região de McMurdo, no Mar de Ross (Anexo 1A, F-G), é desprovida de áreas extensas de afloramento de depósitos datados de idades associadas ao histórico de esfriamento do continente (*e.g.*, Eoceno, Oligoceno e Mioceno).

A região próxima à Baía Prydz (Anexo 1A) contém algumas unidades neogênicas preservando moluscos bivalves. Nas proximidades de Prince Charles Mountains, clastos transportados da Formação Battye Glacier (Mioceno inicial) preservam pelo menos três táxons de bivalves, sendo apenas dois identificados até o nível de gênero (Stilwell *et al.* 2002). Em Marine Plain, Vestfold Hills, rochas do Plioceno inicial contêm bivalves mal preservados, sendo que apenas os pectinídeos foram estudados do ponto de vista taxonômico (Jonkers 2003, Beu & Taviani 2013).

A maior parte do registro oriental da Antártica provém dos “blocos erráticos de McMurdo” (*McMurdo Erratics*), um depósito retrabalhado que, como o próprio nome indica, é constituído principalmente por matacões e blocos. Os fósseis foram coletados de morenas costeiras em Minna Bluff, Mount Discovery, Ilha Black e Península Brown, onde atualmente ocorrem as geleiras Byrd, Skelton e Mulock, na borda da Plataforma de Gelo Ross (*Ross Ice Shelf*; Harwood & Levy 2000; Anexo 1A, F-G). O depósito preserva material temporalmente misturado da Formação Scallop Hill (Plioceno), rochas com idades entre o Eoceno e o Oligoceno, além de depósitos de idade paleozoica provenientes das Montanhas Transantárticas (Harwood & Levy 2000). Os bivalves foram preservados em facies mais proximais de um sistema de leques aluviais deltaicos (fan-deltas), a partir da ação de geleiras durante o Plio-Pleistoceno (mais detalhes e referências adicionais em Stilwell & Feldmann 2000). Tais geleiras teriam escavado material de unidades mais antigas e formado um grande corpo receptor de cerca de 1.000 metros de profundidade, denominado informalmente de “Bacia Profunda Discovery” (*Discovery Deep Basin*; Harwood & Levy 2000). Os bivalves fósseis incluem 32 gêneros, dos quais 24 com atribuição específica (Stilwell 2000). A idade foi atribuída ao Eoceno inicial a médio, com base em exemplares palinológicos e devido à similaridade dos moluscos com aqueles preservados na Formação La Meseta, Ilha Seymour, Península Antártica (Stilwell 2000; Anexo 1A-B). No entanto, muitas das espécies possuem ampla distribuição temporal, o que sugere que esse material paleontológico não possui valor estratigráfico.

Ao contrário dos fósseis preservados nos blocos erráticos, o material proveniente dos testemunhos realizados na região do Mar de Ross, em McMurdo e próximo do Cabo Roberts (*Cape Roberts*) e Ilha Ross (Anexo 1A, F-G) apresentam intervalos de idade mais confiáveis. Os dados são provenientes de testemunhos obtidos na década de 1970 pelo DSDP (*Deep Sea Drilling Project*), 1980 pelos projetos CIROS (*Cenozoic Investigation in the Western Ross Sea*) e, mais

recentemente, pelos projetos contemplados pelo ANDRILL (*Antarctic Geological Drilling*), com atividades de perfuração promovidas pelo CRP (*Cape Roberts Project*). Os testemunhos abrangem sedimentos recentes até rochas eocênicas, com diversas ocorrências de bivalves, alguns dos quais relativamente bem preservados, o que permitiu a identificação taxonômica de vários gêneros e espécies.

Dentre os testemunhos realizados pelo projeto DSDP, dois sítios (270 e 272), alcançando acima de 400 metros de profundidade e idades do Oligoceno ao Mioceno inicial, recuperaram restos fossilizados de bivalves (Hayes *et al.* 1975). Foram identificados 14 táxons dentre espécies e gêneros sem atribuição específica (Dell & Fleming 1975).

O testemunho CIROS-1 alcançou cerca de 700 metros de profundidade e recuperou depósitos do Pré-Cambriano ao Paleozoico, Devoniano ao Cretáceo, sucessões marinas pré-glaciais do início do Paleógeno e sequência glacial do Oligoceno ou final do Eoceno ao Recente (Barrett *et al.* 1989). Estão preservados seis táxons de bivalves, de idades atribuídas ao final do Eoceno e Oligoceno, a maioria com representantes atuais no Oceano Austral (Beu & Dell 1989).

O testemunho CRP-1 abrange sedimentos do Mioceno e Quaternário em profundidades de 147 metros (Cape Roberts Project Science Team 1998). Os exemplares de bivalves provenientes das unidades pleistocênicas são principalmente fragmentos e formas juvenis, mas os mais bem preservados incluem sete espécies e quatro gêneros sem atribuição científica, todos representantes da fauna antártica atual (Taviani *et al.* 1998). Já os exemplares de bivalves do Mioceno inicial correspondem a uma espécie de pectínídeo (Jonkers & Taviani 1998, Jonkers 2003). Já o testemunho CRP-2/2A recuperou uma sucessão do Mioceno ao Oligoceno ao atingir 624 metros de perfuração (Cape Roberts Project Science Team 1999). A fauna de bivalves do Mioceno é bastante restrita, mas a do Oligoceno é representada por centenas de exemplares, a maioria composta por fragmentos, mas alguns completos permitiram a identificação taxonômica de sete gêneros sem atribuição específica (Taviani *et al.* 2000). Por fim, o testemunho CRP-3 alcançou 939 metros de profundidade e recuperou uma sucessão do Oligoceno ao início do Eoceno (Cape Roberts Project Science Team 2000). Os bivalves foram identificados em oito gêneros sem atribuição específica (Taviani & Beu 2001).

Outros registros fósseis de testemunhos na região do Mar de Ross, em McMurdo, possuem idades atribuídas ao Neógeno. Do testemunho ANDRILL-1B provêm diversos fragmentos de bivalves ao longo da sondagem (Scherer *et al.* 2007). No entanto, a baixa preservação materializada principalmente pelo alto grau de fragmentação dificulta a identificação taxonômica dos fósseis. O testemunho AND-2A registra o material mais rico e abundante de macrofósseis de todos os projetos de sondagem da Antártica (Taviani *et al.* 2010, p. 137). Os

bivalves em melhor estado de preservação foram encontrados nas unidades atribuídas ao Mioceno inicial (LSU 7 e LSU 11), identificados em cinco gêneros sem atribuição específica.

As espécies fósseis conhecidas de depósitos cenozoicos da Antártica com seus respectivos dados de proveniência, idade e referência bibliográfica estão listadas no Anexo 2.

3.2. Contexto paleobiogeográfico: estudos prévios

Os moluscos bivalves possuem grande potencial como ferramenta em estudos de distribuição paleobiogeográfica devido à alta probabilidade de preservação, grande abundância e diversidade, bem como a variedade de características ecológicas encontradas no grupo (Kauffman 1973, Kidwell 2005, Valentine *et al.* 2006, Belanger *et al.* 2012).

Trabalhos de campo na ilha Seymour durante a primeira metade da década de 1970 resultaram nos primeiros trabalhos paleobiogeográficos incluindo dados fósseis do Cretáceo, Paleoceno e Eoceno da Antártica. É importante ressaltar que os primeiros estudos sobre a evolução paleogeográfica da Antártica, realizados por Zinsmeister (1979a, b, 1982, 1987), basearam-se em dados paleontológicos, sobretudo no registro de moluscos.

Durante o Mesozoico, a Antártica era parte do Domínio Biogeográfico Temperado Austral, Região Indo-Pacífica, Província Austral (Kauffman 1973). A Província Austral teria se definido no início do Cretáceo era formada pelas Subprovíncias Australiana e da Nova Zelândia, áreas do norte da Austrália (como ilhas da Indonésia, Nova Guiné e Nova Caledônia), além do extremo sul da América do Sul e Antártica.

Embora algumas relações de fauna fossem observadas entre a Província Austral e sul da Índia, esta não era considerada como parte da Província Austral a partir do início e metade do Cretáceo. Além disso, o registro da América do Sul no início da década de 1970 era relativamente escasso e o conhecimento sobre a Antártica era insuficiente para tecer relações faunísticas com as outras áreas austrais. A interpretação foi, portanto, realizada com base nas informações da Austrália e da Nova Zelândia, consideradas como subprovíncias da Província Austral. A evolução tectônica e o subsequente isolamento de massas no final do Mesozoico teriam culminado na separação da Província Austral no final do Cretáceo e início do Paleógeno. Segundo Zinsmeister (1979a), após a separação da Índia, a Província Austral teria sido fragmentada em diversas províncias durante o final do Cretáceo. A maior delas, a Província Weddelliana, teria correspondido à extensa faixa de águas rasas compreendida entre a margem oriental da Austrália,

Nova Zelândia, porção pacífica da Antártica, Península Antártica e sul da América do Sul (Figura 5).

A Província Weddelliana teria existido do final do Cretáceo à metade do Eoceno (Zinsmeister 1979a, b, Stilwell 2003), com persistência de conexão marinha entre a Austrália e a Antártica até a metade do Oligoceno (Exon *et al.* 2001). Após a separação entre a Austrália e a Antártica, a reorganização tectônica na região teria desencadeado nova fragmentação e, consequentemente, alterado o padrão de circulação oceânica e atmosférica, as quais também teriam influenciado as condições ambientais. As novas condições representariam um mecanismo de isolamento, responsável pela nova configuração biótica ao longo do restante do Cenozoico, com o aumento no grau de endemismo em cada uma das regiões (Zinsmeister 1979a, Stilwell 2003).

Figura 5: Reconstituição da Província Weddelliana durante o final do Cretáceo (compilado de Zinsmeister 1979a, 1982 e Lawver & Gahagan 2003).

A despeito dos comentários acima, a dinâmica paleobiogeográfica cenozoica do Oceano Austral não está completamente compreendida. A organização das correntes oceânicas que levaram à formação da Corrente Circum-Antártica durante o Oligoceno (Exon *et al.* 2001, Barker & Thomas 2004) poderia, na verdade, ter favorecido a ocorrência de eventos de dispersão entre a Antártica e regiões periféricas (Crame 1992, 1999). Somente após o completo estabelecimento da Corrente Circum-Antártica, por volta do início ou metade do Oligoceno (Pfuhl & McCave 2005), ou mesmo após o Mioceno médio (Barker & Burrell 1977, Lear *et al.* 2000, Eagles & Livermore 2002), o intercâmbio de faunas teria sido reduzido abruptamente a níveis muito baixos, o que contribuiria para o endemismo da região (Barnes *et al.* 2006).

De fato, Linse *et al.* (2006) reconheceram três províncias biogeográficas modernas na região antártica, de acordo com o registro atual de gêneros e espécies de moluscos: Província Antártica Continental, incluindo todo o continente antártico exceto a península; Província do Mar de Scotia, englobando a Península Antártica; e Província Subantártica, correspondendo às ilhas próximas à Convergência Antártica. Os dados de Linse *et al.* (2006) corroboram a ideia de que a Corrente Circum-Antártica representa atualmente uma barreira para o intercâmbio de faunas entre a região abrangida pela Convergência Antártica e regiões periféricas.

Embora Barnes *et al.* (2006) tenham afirmado que a Antártica teria se configurado em nova província biogeográfica somente após o completo estabelecimento da Corrente Circum-Antártica, Stilwell (2000, 2003) propôs que a Antártica teria se configurado em nova província ainda na metade do Eoceno, com base na observação de 11% de gêneros endêmicos da Formação La Meseta, Ilha Seymour (Anexo 1B), de idade eocênica.

Beu (2009) analisou a similaridade do registro de moluscos em nos depósitos do Paleoceno, Eoceno e Oligoceno-Mioceno da Antártica em relação ao registro de táxons coetários da Nova Zelândia e sul da América do Sul. A proporção de gêneros que vivem atualmente na Antártica e Subantártica aumentou substancialmente no Paleoceno (15%), Eoceno (30%) e Oligoceno-Mioceno (59%), refletindo o progressivo isolamento tectônico e térmico da Antártica.

Considerando que a Antártica se configurou em nova província biogeográfica no Eoceno (Stilwell 2000) ou mesmo após o Oligoceno final (Barnes *et al.* 2006), é esperado que o número de táxons compartilhados entre a Antártica e outras regiões do Oceano Austral tenha diminuído ao longo do Cenozoico. Neste caso, a reorganização do regime de correntes oceânicas durante o Neógeno até os padrões modernos de circulação, com a formação da Corrente Circum Antártica e a Frente Polar (Anexo 1A) teria configurado uma barreira para o intercâmbio de faunas entre a Antártica e regiões periféricas, e representaria, portanto, um mecanismo de isolamento. Alguns estudos com base em relógio molecular sugerem a ocorrência de eventos vicariantes de táxons marinhos austrais da Antártica e Subantártica entre o Mioceno e o Plioceno (Patarnello *et al.* 1996, Page and Linse 2002, González-Wevar 2012).

Por outro lado, o registro cenozoico de alguns táxons de bivalves e braquiópodes do Oceano Austral sugere que a reorganização das correntes oceânicas teria favorecido o surgimento de rotas migratórias entre as porções pacífica e atlântica da Antártica, num padrão associado às duas fases do desenvolvimento da Corrente Circum-Antártica (Quaglio *et al.* 2008). Neste caso, portanto, o estabelecimento de correntes frias em torno da Antártica teria representado um mecanismo de dispersão, entendido como aumento da área de distribuição de organismos marinhos após a eliminação de uma barreira geográfica ('geodispersão', Lieberman & Eldredge 1996).

Considerando o registro cenozoico de gêneros de bivalves em comum entre a Nova Zelândia e Antártica, quase a metade dos táxons sugere eventos de dispersão da Antártica para a Nova Zelândia ainda durante o Eoceno (Quaglio 2007). O padrão de distribuição desses táxons apoia a hipótese da existência de conexões marinhas de plataforma rasa entre o oeste e o leste da Antártica ("Passagem de Shackleton" de Zinsmeister 1979b, Stilwell 1996) e da Província Weddelliana (Zinsmeister 1979a, b, Stilwell 2003; Figura 5) do final do Cretáceo ao Eoceno. A dispersão teria ocorrido durante o Eoceno, segundo a reconstituição proposta por Lawver & Gahagan (2003), mas no sentido Atlântico-Pacífico, como sugerido por Lazarus & Caulet (1993). A outra metade dos gêneros registrados sugere dispersão da Antártica para a Nova Zelândia após o Oligoceno inicial. A dispersão desses táxons ocorreu provavelmente durante o estabelecimento da Corrente Circum-Antártica (~24 Ma, Pfahler & McCave 2005), margeando a Antártica pelas bordas ocidental atlântica e oriental em direção à Nova Zelândia.

Este mesmo padrão foi observado ao se rastrear o registro cenozoico de gêneros de bivalves da Ilha Rei George Antártica desde o final do Cretáceo ao Recente (Quaglio *et al.* 2007b). Onze gêneros apresentaram informação da dinâmica paleobiogeográfica em quatro intervalos de tempo: do final do Cretáceo ao início do Eoceno, do final do Eoceno ao início do Oligoceno, do início do Oligoceno ao início do Mioceno e do início do Mioceno ao Presente. O padrão de distribuição observado temporalmente entre cada um dos intervalos sugere que cada representante com registro mais antigo em determinada localidade surge em outra localidade no intervalo seguinte em sentido horário geograficamente. Além disso, as ocorrências mais novas são registradas em duas fases: a primeira na porção pacífica (do final do Cretáceo ao início do Oligoceno) e a segunda na porção atlântica do Oceano Austral (do início do Oligoceno ao Presente). O padrão de distribuição temporal do registro fóssil concorda com as fases de reorganização das correntes oceânicas e o estabelecimento da Corrente Circum-Antártica.

Essa interpretação é corroborada por diversos estudos que abordaram a participação de eventos de dispersão na distribuição biogeográfica. Por exemplo, Queiroz (2005) listou exemplos nos quais eventos de dispersão oceânica explicam o padrão de distribuição de diversos táxons atuais. Sanmartín & Ronquist (2004), com base na análise de vicariância-dispersão de 73 filogenias disponíveis de plantas e animais, concluíram que o padrão de distribuição do hemisfério sul tem maior participação de eventos de dispersão do que vicariância pela quebra do Gondwana.

Na região austral, Beu *et al.* (1997) realizaram estudo comparativo entre o registro cenozoico de moluscos em comum entre a Nova Zelândia e América do Sul. A análise evidenciou o grande número de táxons cujo registro aponta para dispersão da Nova Zelândia para a América do Sul entre o final do Oligoceno e início do Mioceno. De acordo com os

autores, os táxons teriam dispersado durante a fase de estabelecimento da Corrente Circum-Antártica, pela margem ocidental pacífica da Antártica. Número menor de táxons teria dispersado da América do Sul para a Nova Zelândia, também no intervalo entre o final do Oligoceno e início do Mioceno. Neste caso, a dispersão teria ocorrido após a abertura da passagem de Drake, mas da margem ocidental atlântica da Antártica para a margem oriental pacífica em direção à Nova Zelândia.

Esse cenário de evolução paleobiogeográfica com base em dados paleontológicos é corroborado por evidências de grupos marinhos atuais capazes de transpor a barreira da Frente Polar e Corrente Circum-Antártica (veja exemplos em Clarke *et al.* 2005).

4. Materiais e MÉTODOS

4.1. Fósseis estudados

Foram estudados quatro conjuntos de materiais referentes a bivalves provenientes dos depósitos cenozoicos da Ilha Rei George, Antártica, a saber:

- 1) Formação Destruction Bay (Oligoceno inicial), exemplares de pectinídeos coletados por A. Gaździcki, e que foram trazidos ao Brasil após visita ao *Instytut Paleobiologii* (PAN) em Varsóvia, Polônia, destinados ao estudo taxonômico;
- 2) Formação Cape Melville (Mioceno inicial), exemplares de nculídeos coletados pela equipe do *British Antarctic Survey* (BAS), em Cambridge, Reino Unido, depositados na mesma instituição, bem como exemplares coletados por L.E. Anelli (IGc/USP), depositados no Laboratório de Paleontologia de Invertebrados do Instituto de Geociências da USP (LPS). Este material foi estudado taxonomicamente;
- 3) Formação Cape Melville (Mioceno inicial), exemplares de periplomatídeos e limopsídeos, coletados por A. Gaździcki e trazidos ao Brasil das coleções do PAN, e um exemplar de limatulídeos, coletado pela equipe do BAS, destinados ao estudo taxonômico e paleobiogeográfico ;
- 4) Membro Low Head, Formação Polonez Cove (Oligoceno inicial), região de Low Head, material amostrado nos níveis de coquina da unidade coletado por L. E. Anelli (IGc/USP) e depositado no LPS, além de exemplares medidos e fotografados durante a visita ao PAN, estudados do ponto de vista tafonômico.

4.1.1. Preparação

Os exemplares destinados aos estudos taxonômicos foram preparados com a remoção cuidadosa dos restos de sedimento e rocha sob lupa *Leica MZ95* e iluminador *Leica CLS 100X* com o auxílio de micropercussiva *Powerline 72* e instrumental odontológico e de relojoaria. Já os espécimes estudados tafonomicamente foram removidos da matriz de rocha com auxílio de martelo e cinzel. A morfologia foi posteriormente estudada sob lupa e iluminador. Os exemplares receberam camada delgada de tinta *Nankin* com auxílio de pincel. Após secagem completa, foram recobertos por magnésio metálico para realçar feições morfológicas internas e externas das conchas.

Os exemplares periplomatídeos da Formação Cape Melville se tratam de moldes articulados fechados, dificultando a possível visualização do condróforo, estrutura internalizada

da concha imprescindível para o reconhecimento taxonômico. Por este motivo, um espécime foi submetido ao método de seção seriada. Previamente ao desgaste, foram marcadas linhas perpendiculares ao plano de comissura do exemplar. O desgaste foi realizado a partir da valva esquerda em placa de vidro com carbetto de silício pulverizado (SiC), paralelamente ao plano de comissura demarcado pelas linhas. Durante o desgaste, foram capturadas imagens das seções para o reconhecimento da presença do condróforo e posterior desenho esquemático.

Os exemplares que possuíam feições em escala nanométrica, como microestrutura externa da concha, foram levados ao Microscópio Eletrônico de Varredura *LEO 440 I* do Laboratório de Microscopia Eletrônica de Varredura do IGc/USP. Para a preparação, fragmentos dos exemplares foram removidos e montados em *stubs* com fita de carbono ou cola, e recobertos por camada de ouro.

Para a captura de imagens, os exemplares foram adequadamente iluminados por luz fria para ressaltar as feições taxonômicas preservadas em relevo, como ornamentação externa, dentição e cicatrizes musculares. Posteriormente, os espécimes foram fotografados com câmera digital *Canon EOS Rebel T3* acoplada à lente macro de 100mm. As imagens foram tratadas nos softwares *Corel Photopaint X5* e *Corel Draw X5*.

Todo o instrumental de limpeza mecânica e captura de imagens pertence ao Laboratório de Paleontologia de Invertebrados do IGc/USP.

4.1.2. Descrições taxonômicas e tafonômica

As descrições taxonômicas foram realizadas a partir do estudo minucioso de caracteres morfológicos dos exemplares e comparação com espécimes fósseis e viventes de grupos relacionados. O estudo tafonômico envolveu a construção de tabela de assinaturas tafonômicas. Mas detalhes sobre os métodos de estudo estão pormenorizados nos anexos 3-5.

4.2. Levantamento e atualização do registro paleontológico

Para as análises paleobiogeográficas, foi estudada extensa lista de gêneros de bivalves fósseis e atuais. O registro paleontológico analisado compreendeu táxons preservados em depósitos do Cretáceo ao Pleistoceno, de latitudes atualmente mais altas do que 34°, que incluíram dados do sul da África do Sul, Austrália, Nova Zelândia, Antártica e sul da América do Sul.

Os dados fósseis foram obtidos nas seguintes bases de dados: SOMBASE-GSCM (*the Cenozoic Marine Fauna Database*, Griffiths *et al.* 2003), *the Paleobiology Database* (<http://paleodb.org>),

além de outras referências cujos dados estavam ausentes em ambas as bases (*eg.* Griffin & Pastorino 2006, Aguirre *et al.* 2008, Quaglio *et al.* 2008, 2010, Whittle *et al.* 2011, 2012, Beu 2009, Beu & Raine 2009, Beu & Taviani 2013). Especial atenção foi dada aos dados da Antártica, foco desta tese. Os dados obtidos das bases foram atualizados a partir de levantamento realizado previamente (Quaglio 2007), acrescidos de novas informações da literatura (Anexo 2). Os dados recentes foram obtidos de “SCAR Mar-BIN” (<http://www.scarmarbin.be/>), OBIS (www.iobis.org) e Spencer *et al.* (2011).

4.3. Análises paleobiogeográficas

De acordo com Crisci *et al.* (2003), a biogeografia é um campo das ciências cuja definição é relativamente simples: o estudo da distribuição geográfica dos seres vivos. Entretanto, por ser um tema naturalmente interdisciplinar ao incluir conceitos das ciências geológicas, geográficas e biológicas, é marcado por grande complexidade. Isto se deve também ao fato de que o interesse pelos padrões de distribuição dos organismos e pelos mecanismos deflagradores dessa distribuição surgiu sincronicamente com a formalização da classificação taxonômica dos organismos propriamente. Desde a formalização da classificação binomial de Lineu, estudos biogeográficos já se faziam presentes (Humphries 2002).

Mais recentemente, no entanto, maior interesse tem sido dispensado à biogeografia, em decorrência do desenvolvimento do método cladístico no contexto da sistemática filogenética, com a publicação de W. Hennig e, após as publicações de L. Croizat sobre a panbiogeografia (Humphries 2002).

4.4.1. Histórico

Historicamente, foram dois os momentos dentro da disciplina biogeográfica que definiram duas principais escolas teóricas. À época de Lineu, prevaleciam as ideias, geralmente baseadas em conceitos religiosos, de que os organismos surgem em uma determinada região, denominada “Centro de origem”, a partir da qual dispersam para áreas contíguas (Craw *et al.* 1999, Crisci *et al.* 2003). C. Darwin e A. R. Wallace sustentavam que a especiação era promovida pela dispersão de espécies a partir de pontos centrais de origem e que tal fenômeno era fundamental na evolução em escala de tempo geológico (MacDonald 2003).

Diversos pesquisadores trabalharam dentro do paradigma do dispersalismo. G. L. Leclerc, o conde de Buffon, ao considerar o conceito dos centros de origem, concluiu que as espécies se modificam por degeneração quando expostas a condições ambientais extremas (*vide* Briggs & Humphries 2004). Outros pesquisadores também fundamentaram seus estudos no conceito de dispersalismo, dentre os quais, P. A. Latreille (Dupuis 1974), A. Von Humboldt, G. Cuvier (Briggs & Humphries 2004), e, mais recentemente, Briggs (2003).

Ainda dentro desse paradigma, A. P. de Candolle em 1820 introduziu dois novos termos para distinguir dois campos de atuação da biogeografia, denominados “estação” e “habitação” (Briggs & Humphries 2004). O primeiro diz respeito às características ecológicas do local, enquanto o segundo relaciona-se à geologia e geografia daquela área. Assim, as interpretações a partir da visão da biogeografia ecológica estão associadas a causas físicas atuando no presente, enquanto que as explicações dentro da biogeografia histórica dependem de causas que existiram no passado (Crisci *et al.* 2003).

O grande desenvolvimento dos conceitos biogeográficos se deu a partir da mudança de paradigmas dentro das biociências (com a sistemática filogenética) e geociências (com a tectônica global), as quais Crisci *et al.* (2003) chamaram de “forças externas”, que impulsionam o desenvolvimento da biogeografia. O primeiro conceito, introduzido ainda no começo do século XX, mas aceito somente após a década de 1960, passou a representar um contexto inédito para o estudo do padrão de distribuição dos organismos, sobretudo como parte da biogeografia histórica: a Teoria da Deriva Continental de A. Wegener (Giller *et al.* 2004), embrião do que viria a ser a Tectônica Global. O entendimento da dinâmica das massas de terra, representada pela abertura e fechamento de bacias oceânicas e o surgimento ou desaparecimento de conexões marinhas e terrestres, imprimiram novas leituras e interpretações sobre a evolução dos padrões de distribuição dos organismos, principalmente no campo da biogeografia histórica.

Outra mudança profunda que impulsionou o desenvolvimento da biogeografia foi o surgimento dos métodos de análise filogenética para o estudo das relações de parentesco entre os organismos (Hennig 1966). Com esses novos métodos, as interpretações dos padrões de distribuição passaram a ser feitas também com base nas relações filogenéticas dos grupos estudados, uma vez que a evolução biológica está intimamente ligada à geológica. A partir da criação dessa nova escola, e principalmente com o desenvolvimento de métodos estatísticos aplicáveis à análise cladística, a biogeografia passou a contar com técnicas analíticas de estudo de distribuição, as quais inferem sobre uma ou mais causas responsáveis pelo mesmo padrão de distribuição observado em vários grupos (Funk 2004).

A principal mudança conceitual para a biogeografia após o surgimento da sistemática filogenética foi a ideia de vicariância como processo causal da diversidade (Funk 2004). Assim, a

especiação de um ou mais organismos ocorre em resposta ao isolamento geográfico do grupo, representado como fragmentação da área. Eventos de especiação identificados por cladogênese nos cladogramas taxonômicos podem ser associados à vicariância. Dessa forma, a representação diagramática nos táxons terminais dos cladogramas taxonômicos pode ser interpolada pelas áreas de ocorrência desses táxons, gerando cladogramas representativos da evolução de fragmentação das áreas consideradas ancestrais – os cladogramas de área (MacDonald 2003).

4.3.2. Algumas definições

No entanto, até mesmo os conceitos de biogeografia têm sido objeto de intenso debate. Não é raro observar na literatura o emprego do mesmo termo, mas com conceitos diversos. Como detalhado a seguir, alguns termos podem ser considerados contraditórios ou exclusivos entre si por alguns autores, complementares, ou mesmo parcialmente sobrepostos por outros grupos de pesquisadores. Seguem abaixo alguns dos conceitos importantes utilizados nas abordagens biogeográficas.

Área e padrão de distribuição

De acordo com Cain (Funk 2004), a área de distribuição é a região dentro da qual uma unidade taxonômica está distribuída ou presente. Geralmente, é delimitada por fatores ambientais, como clima (temperatura e umidade) e habitat, além de fatores ecológicos, como competição, predação e outras relações ecológicas. A representação é feita por meio de mapas utilizando-se pontos, contorno manual, quadriculas ou mesmo aglomerados de pontos de ocorrência plotados usando-se a relação da distância entre os pontos (Crisci *et al.* 2003). Uma vez que é realizada com base em esforço de coleta e dados disponíveis na literatura, os mapas de áreas de distribuição refletem o estado do conhecimento sobre o grupo em estudo.

O padrão de distribuição é obtido a partir da coincidência na distribuição espacial de vários táxons, a qual pode refletir uma história em comum entre os grupos. No entanto, Donoghue & Moore (2003) sugeriram que um padrão coincidente deve ser estudado também do ponto de vista temporal, já que determinado evento pode afetar de forma distinta dois ou mais grupos. Esta influência heterogênea pode gerar resultados “falsos-positivos” ou falsos-negativos” durante a comparação dos padrões de distribuição. Daí a importância da coincidência ou não ser confirmada com dados de paleontologia ou biologia molecular para se atestar a “homologia espacial” – também chamada de congruência – entre os padrões de distribuição encontrados.

A plotagem da área de distribuição é geralmente utilizada em algumas técnicas de análise de parsimônia de endemidade (Crisci *et al.* 2003), mas a interpretação de padrões de distribuição é bastante comum na biogeografia cladística (Donoghue & Moore 2003). O método de inserção dos pontos depende do programa utilizado na análise.

Área de endemismo

De acordo com Nelson & Platnick (1981), áreas de endemismo são definidas como regiões ou áreas relativamente pequenas contendo número significativo de espécies que não ocorrem em outras áreas. Para Harold & Mooi (1994), área de endemismo corresponde a uma região geográfica que compreende dois ou mais táxons monofiléticos exibindo congruência distribucional e filogenética, e cujos táxons aparentados ocorrem em outras regiões definidas como tal. Morrone (1994), porém, define como área de congruência distribucional não aleatória entre diferentes táxons. No entanto, como já destacado anteriormente, a simples coincidência entre a ocorrência de táxons pode não ser resultado de uma história biogeográfica comum. Conforme mencionado previamente, Donoghue & Moore (2003) sugeriram a inclusão de dados paleontológicos e moleculares para a confirmação da coincidência entre os padrões de distribuição, o que implica em um método de verificação se os grupos analisados sofreram a mesma história biogeográfica. De fato, Morrone (2001) aplicou a ideia de homologia primária e secundária da definição de caracteres homólogos, sob o enfoque cladístico proposto por Pinna (1991), para as áreas de distribuição biogeográfica. De forma geral, a homologia espacial primária se refere a um histórico biogeográfico conjectural comum entre os grupos, enquanto a homologia espacial secundária corresponde ao teste cladístico da homologia previamente hipotetizada. Morrone (2001) concluiu ainda que a panbiogeografia lida com homologia primária, enquanto os métodos de biogeografia cladística lidam com a homologia secundária.

Morrone (1994) propôs um método de identificação de áreas de endemismo com base na análise de parcimônia de dados de ocorrência delimitados por quadrículas. O resultado obtido pode ser comparado com análises de outros grupos para a mesma região em estudo.

Segundo Harold & Mooi (1994), o reconhecimento de áreas de endemismo pode ser realizado em duas fases. A primeira é feita com base na área de distribuição, a partir da qual são construídas hipóteses para as relações entre os táxons e posteriormente delimitadas suas distribuições. A segunda fase envolve a adição de táxons não contemplados na primeira fase com o objetivo de serem identificados padrões de distribuição coincidentes e possíveis áreas de endemismo. Além disso, os autores propuseram que as distribuições não congruentes não devem ser consideradas como tais se houver evidência geológica de que a região teve história geográfica única.

Szumik & Goloboff (2004) propuseram um método de quadrículas sobre um sistema cartesiano, no qual são esperadas três categorias como critérios de reconhecimento: espécies ausentes, presentes e assumidamente presentes. As espécies são categorizadas de acordo com a distribuição no conjunto de quadrículas. Assim, espécies distribuídas em quadrículas próximas são consideradas mais potencialmente endêmicas do que aquelas distribuídas amplamente no conjunto de quadrículas.

Como será visto a seguir, a delimitação de áreas de endemismo é mais amplamente empregada previamente aos métodos de biogeografia cladística, enquanto que a panbiogeografia não requer necessariamente a análise prévia para a delimitação de áreas de endemismo. No então, Crisci *et al.* (2003) observaram que mesmo a panbiogeografia inclui o conceito de áreas de endemismo, ao utilizar os traços generalizados na delimitação de áreas biogeográficas.

Dispersão versus Vicariância

As disjunções são padrões de distribuição heterogêneos observados na área delimitada para estudo e podem ser explicados por três eventos: extinção, vicariância e dispersão. A extinção, definida como a morte de todos os representantes de um determinado táxon, é um processo previsto nas interpretações biogeográficas (Crisci *et al.* 2003), sendo ela narrativa ou analítica, ecológica ou histórica (mas veja discussão de Lieberman 2002).

Já a vicariância e a dispersão implicam na presença de grupos ou populações distintos isolados por uma barreira geográfica (Nelson & Platnik 1981). Porém, a vicariância é o processo pelo qual um táxon sofre especiação quando geograficamente isolado de seu grupo ancestral. Já a dispersão é mais amplamente entendida como duas variantes: migração de representantes para uma área anteriormente não ocupada devido à transposição de barreira (do inglês *dispersal*), ou aumento da área de distribuição de um táxon (do inglês *dispersion*) (Ronquist 1997, Contreras-Medina *et al.* 2001). A grande diferença entre vicariância e dispersão é que, na explicação com base em evento vicariante, existe a premissa na qual a população ancestral ocupava toda a área estudada, enquanto que o evento dispersivo implica na premissa de que a população ancestral não ocupava toda a área de distribuição dos táxons ou populações diferenciados (Figura 6).

No entanto, o conceito de transposição de barreira como mecanismo dispersivo implica em um problema de lógica epistêmica. Afinal, se uma “barreira” pode ser transposta por um grupo de organismos, é porque, no momento da transposição, ela não representa um obstáculo para a passagem daquele grupo e naquele momento específico. Dessa forma, um grupo de organismos ou população isolados por uma barreira - a qual pode ser geográfica, climática, etc. - é capaz de aumentar sua área de ocupação somente quando do desaparecimento da barreira. O evento

vicariante ocorre posteriormente, caso haja o reaparecimento de outra barreira. De fato, Lieberman & Eldredge (1996) propuseram o termo geodispersão (do inglês *geodispersal*), que diz respeito ao desaparecimento de uma barreira, ocupação da área e posterior surgimento de nova barreira produzindo vicariância (Figura 7). Muito embora Lieberman & Eldredge (1996) tenham criado outro termo para a explicação do surgimento e desaparecimento da barreira, o uso do termo dispersão como aumento de área de distribuição seria suficiente para a explicação de toda a dinâmica colocada pelos autores. Assim, poder-se-ia aceitar apenas o conceito de aumento de área de distribuição (*dispersion*) e se evitaria considerar os termos dispersão e vicariância como concorrentes ao se explicarem os padrões de disjunção. Dessa forma, ambos poderiam ser empregados como processos complementares nos eventos de ocupação de área e posterior especiação.

Figura 6: Processos espaço-temporais para explicar disjunções: vicariância e dispersão. A especiação por vicariância implica na ocupação total da área previamente ao surgimento da barreira. A especiação por dispersão implica na transposição de uma barreira geográfica para a ocupação de nova área (modificado de Crisci *et al.* 2003).

Hallam (1981, p. 340) considerou a vicariância e a dispersão como fenômenos igualmente importantes e “dois lados da mesma moeda”. Frente a isso, a polêmica envolvida na conceituação vicariância *versus* dispersão é desnecessária se o termo ‘dispersão’ for definido como aumento de área de ocupação. De maneira mais ampla, pode ser considerado como o conceito de geodispersão de Lieberman & Eldredge (1996), assim como Hallam (1981) havia entendido. Craw

et al. (1999) também assumiram cenários com eventos de dispersão seguidos de vicariância no modelo biogeográfico chamado ‘modelo gerador de forma vicariante’ (do inglês *vicariant form-making model*), no qual há alternância de fases de ‘mobilismo’, quando as formas ancestrais dispersam e aumentam a área de ocupação, e ‘imobilismo’, quando as formas ancestrais sofrem vicariância e geram formas descendentes com área de ocupação restrita.

Figura 7: Processo espaço-temporal para explicar disjunções: geodispersão. A população ocupa nova área somente após o desaparecimento da barreira, quando ocorre a dispersão. Posteriormente, nova barreira surge e a população sofre especiação por vicariância (de acordo com Lieberman 2000). Note-se que os termos vicariância e dispersão são complementares para a explicação do processo.

Sob o mesmo enfoque, Lieberman (2003) listou diversos estudos biogeográficos com base em dados fósseis – ou paleobiogeográficos – nos quais as conclusões apontam para um cenário de alternância entre fases de vicariância e aumento de área de distribuição. Segundo o autor, esse fenômeno é observado após a análise (paleo)biogeográfica do registro fóssil de dinossauros, mamíferos, peixes, artrópodes, incluindo trilobites, crustáceos e insetos.

Outro exemplo de como eventos de dispersão ocorre com a eliminação de uma barreira geográfica citado por Lieberman (2008) é o chamado Grande Intercâmbio Biótico Americano (Giller *et al.* 2004). Neste exemplo, a presença de táxons aparentados no norte e sul do continente americano é explicada por um evento de dispersão ocorrido entre o final do Plioceno e início do Pleistoceno. Com isso, alguns tetrápodes da América do Norte e América do Sul alcançaram, respectivamente, o sul e o norte após a eliminação de uma barreira geográfica para organismos terrestres. Esta, representada pela confluência entre o Mar do Caribe e o Oceano Pacífico, foi eliminada com o surgimento do Istmo do Panamá. Este cenário é corroborado pela evidência da formação do Istmo do Panamá à época do evento e a ausência de fósseis sul-americanos de idade anterior ao Plioceno final na América do Norte, e de norte-americanos na América do Sul. No entanto, alguns autores, como Crisci *et al.* (2003), consideram este um exemplo de explicação dispersialista, sob o enfoque de centro de origem (veja a seguir).

4.3.3. Uso de dados fósseis: a Paleobiogeografia

Dentre a os biogeógrafos responsáveis pela produção da literatura científica atual, Lieberman (1997, 2000, 2002, 2003, 2008) é um dos poucos defensores da importância da paleontologia e dos dados fósseis nos estudos analíticos de biogeografia. Em seus trabalhos, costuma aplicar o termo paleobiogeografia, quando os dados utilizados nas análises contemplam total ou parcialmente informações do registro fóssil.

A despeito da natureza dos dados – se provenientes do registro atual ou fóssil –, o emprego de uma ou outra abordagem vai depender principalmente da disponibilidade de análises cladísticas prévias para o grupo estudado. No entanto, é ainda necessário que tenham sido gerados cladogramas com boa resolução topológica para a interpretação das hipóteses biogeográficas nos cladogramas de área (S. Nihei, comunicação verbal, 2009). Por este motivo, algumas técnicas não são aplicáveis para determinados grupos.

No caso de organismos fósseis – cujos estudos mais raramente geram cladogramas de boa resolução em relação aos produzidos com base em caracteres de organismos recentes – podem ser empregados os métodos de panbiogeografia e análise de parcimônia de endemidade. As técnicas relativas a essas abordagens têm por objetivo a delimitação de possíveis áreas de endemismo ou o encontro de padrões distribucionais associados a determinado evento geológico (Lieberman 2000, Posadas *et al.* 2006, Nihei 2006). A análise biogeográfica dos grupos tem um papel secundário com o emprego desses métodos, sendo o foco principal o estudo da área de distribuição (Crisci *et al.* 2003).

Ainda assim, existem alguns exemplos de aplicação de dados fósseis em análises biogeográficas, incluindo a geração de cladogramas taxonômicos. Em um dos seus estudos de biogeografia filogenética, Lieberman (1997) propôs um modelo de evolução paleogeográfica para o início do Cambriano com base na topologia das relações filogenéticas de trilobitas olenelídeos e análise de parcimônia de Brooks para as inferências biogeográficas do grupo. Os resultados apontaram para a maior influência de eventos vicariantes no padrão de distribuição, o que implica na confirmação de eventos de rifteamento durante o intervalo analisado. Além disso, a interpretação aponta para a separação entre a Laurásia e Báltica previamente à separação entre a Laurásia e a Sibéria.

Mais recentemente, Lieberman (2002) comparou resultados de análises hipotéticas realizadas somente com base em dados fósseis, somente com base em dados recentes e incluindo tanto dados fósseis como recentes. Os resultados apontaram para maior resolução dos padrões de distribuição com o emprego de ambos os dados em relação àqueles utilizando-se apenas um ou outro tipo de dados. Enquanto as análises a partir de dados recentes geram mais

incongruências artificiais (extinções não-naturais), análises com base em fósseis podem resultar em cladogramas não sustentados devido à escassez de dados inerente ao registro fóssil. Muito embora o objetivo central do trabalho fosse avaliar a influência das extinções na resolução das incoerências dos cladogramas de área, o autor concluiu que a inclusão de dados paleontológicos nas análises adiciona informações importantes para as inferências paleobiogeográficas.

4.3.4. Abordagens utilizadas

Conceitos

De acordo com diversos autores, entre eles Contreras-Medina *et al.* (2001), Crisci *et al.* (2003) e Posadas *et al.* (2006), são reconhecidas pelo menos 33 técnicas analíticas para estudos biogeográficos distribuídas em nove abordagens. As premissas e os conceitos que definem cada uma das abordagens biogeográficas são diversos, variando de acordo com os paradigmas dentro das geociências e biociências de cada época em que se desenvolveu. De forma geral, a aplicação de um ou outro método depende diretamente da natureza dos dados e o enfoque dado ao estudo (paleo)biogeográfico. Como visto anteriormente, a maior parte dos estudos biogeográficos com base em dados fósseis e recentes de moluscos da Antártica foi realizada sob o enfoque narrativo da biogeografia. Isto, em parte, deve-se ao fato de que o registro fóssil dessa região é pouco conhecido (Quaglio *et al.* 2007a), o que impede o emprego de técnicas que exijam grande número de dados.

Além disso, os moluscos formam um grupo com grande potencial de adaptação ao meio ao apresentarem diversas feições ou caracteres homoplásticos, os quais refletem convergência adaptativa (Stanley 1970; Simões *et al.* 2000). Como consequência, raramente são gerados cladogramas de topologia resolvida em análise filogenética com base em caracteres morfológicos de moluscos (veja exemplo em Simões *et al.* 2000). Frente a isso e considerando o objetivo principal da presente tese, buscaram-se na literatura os métodos analíticos de biogeografia histórica para a aplicação das técnicas adequadas à natureza dos dados, os quais independem da filogenia do grupo.

Panbiogeografia

A panbiogeografia foi criada na década de 1960 por Léon Croizat e se baseia nos princípios de que os organismos e suas áreas evoluem em conjunto e que o entendimento da localidade é fundamental para qualquer análise adequada dos padrões e processos responsáveis pela evolução

(Craw *et al.* 1999, Llorente *et al.* 2000, Grehan 2001). Uma característica do método que aumenta seu potencial de aplicação é a ausência de premissa (dispersão ou vicariância) para a explicação dos padrões de distribuição (Craw *et al.* 1999). De acordo com Crisci *et al.* (2003), a abordagem proposta por L. Croizat representa a integração dentro do campo da biologia comparativa, ao considerar que a diversidade biológica vista como fato histórico ocorre em três dimensões: forma, tempo e espaço. A forma, representada pela sistemática (taxonômica e filogenética), engloba tanto caracteres fenotípicos quanto genotípicos, enquanto o tempo é caracterizado pela paleontologia e embriologia, e o espaço é qualificado pela biogeografia.

O método consiste na construção de mapas de ocorrência dos organismos a partir dos quais são conectadas áreas de distribuição disjuntas por meio de linhas, denominadas traços. Os traços individuais são representados por linhas entre as menores distâncias de ocorrências e correspondem às coordenadas espaciais de um táxon. Traços individuais de grupos não relacionados são superpostos e, caso coincidam, são considerados traços generalizados. Os traços generalizados indicam a existência pretérita de grupos ancestrais, os quais foram fragmentados por eventos tectônicos ou mudanças climáticas. A orientação dos traços pode ser feita por meio da chamada linha de base, que é uma localidade onde existe a correspondência entre um ou mais traços e uma feição geológica, geográfica ou geomorfológica. A presença da linha de base sugere que a distribuição encontrada foi influenciada por aquela determinada feição, e pode ser considerada homologia espacial.

As áreas onde os traços generalizados se interceptam são denominadas nó. A presença de nós sugere que diferentes fragmentos bióticos e geológicos ancestrais ocorreram relacionados espaço-temporalmente, geralmente como consequência de eventos de colagem de terrenos tectonoestratigráficos distintos. Portanto, os nós são limites biogeográficos onde fragmentos residuais de grupos de ancestralidades distintas entraram em contato.

Análise de Parcimônia de Endemicidade (PAE)

Esta abordagem classifica localidades, quadrantes ou áreas de acordo com os táxons presentes. De forma geral, pode ser comparada ao método de análise filogenética, se forem consideradas as áreas da PAE como os táxons da análise filogenética, e os táxons da PAE como os caracteres da análise filogenética (“sinapomorfias”, Nihei 2006). Proposta por Rosen (1988), a técnica foi inicialmente aplicada a dados paleontológicos de um mesmo horizonte estratigráfico. A matriz de táxons deve ser construída de acordo com a presença (1) ou ausência (0) de cada táxon nas áreas analisadas. Após a construção da matriz, os táxons que ocorrem em somente uma área devem ser eliminados por não serem informativos do ponto de vista biogeográfico, as localidades contendo presenças raras devem ser eliminadas por serem consideradas primitivas

pelo método da análise, e as localidades que contêm exatamente os mesmos táxons devem ser consideradas como área única. Os dados são analisados através de programas de algoritmo de máxima parcimônia.

Uma variação da técnica de Rosen (1988) envolve a delimitação prévia das áreas de endemismo e a atribuição da presença de cada táxon nas áreas considerada como caráter multiestado, de acordo com as relações filogenéticas do grupo (Crisci *et al.* 2003). Assim, a táxons monofiléticos é atribuída presença em estado 1, a táxons parafiléticos aos monofiléticos é atribuída presença em estado 2, a táxons polifiléticos formando grupos parafiléticos com os táxons de estado 2 é atribuída presença em estado 3, e assim por diante. Assim como na PAE de Rosen (1988), os dados são analisados através de programas de algoritmo de máxima parcimônia.

Outra variante da PAE é a técnica já mencionada de Morrone (1994) para a delimitação de áreas de endemismo.

Métodos

Para as análises de cluster e PAE, uma matriz de presença (1) e ausência (0) foi gerada a partir dos dados de registro, com 38 localidades/intervalos de tempo X 908 gêneros para as análises de cluster e PAE.

Panbiogeografia: os dados de registro foram plotados como traços individuais sobre reconstituições paleogeográficas do Cretáceo final o Recente, de acordo com os conceitos propostos por L. Croizat e Craw *et al.* (1999), para a visualização da dinâmica distribucional ao longo dos intervalos de tempo.

Cluster: a matriz foi analisada com o *software* PRIMER v6 (Clarke & Gorley 2006) para examinar a similaridade total por localidade/intervalo de tempo, utilizando o método SIMPER (Clarke 1993), a partir de dados de presença não transformados comparados com similaridade de Bray-Curtis (Bray & Curtis 1957).

PAE: um grupo artificial com dados de ausência foi adicionado à matriz de dados previamente à análise. A matriz foi analisada com o *software* Winclada v.1.00.08 (Nixon 2002). As buscas heurísticas foram realizadas em TNT v.1.1. (Goloboff *et al.* 2008). Os cladogramas de área não foram gerados analisando-se as áreas temporalmente, como inicialmente proposto (Rosen 1988, Rosen & Smith 1988, veja também Nihei 2006), mas se considerando todos os intervalos de tempo de cada localidade como diferentes “áreas atemporais”, de forma que a relação temporal entre as localidades integrou a análise.

5. RESULTADOS

Apresentam-se como resultados da presente tese cinco artigos, dos quais dois estão publicados nos periódicos *Antarctic Science* e *Polish Polar Research*, um submetido na *Antarctic Science* e dois em fase final de preparação. Os estudos foram desenvolvidos a partir de materiais de depósitos relacionados aos principais eventos de glaciação na Antártica, ocorridos no Oligoceno e Mioceno. Embora os cinco artigos estejam relacionados ao estudo de bivalves antárticos, um deles trata de tema tafonômico e sedimentológico de uma das mais importantes assembleias fósseis da Antártica, na qual conchas de bivalves são predominantes. Os demais estão diretamente vinculados aos objetivos centrais da tese: a descrição taxonômica de novas espécies cenozoicas e o estudo da distribuição paleogeográfica do registro austral de bivalves cenozoicos. Maiores detalhes sobre as descrições dos resultados estão pormenorizados nos anexos 3-7.

5.1. Tafonomia dos pectinídeos da Formação Polonez Cove

Resumo do artigo “SHELL BEDS FROM THE LOW HEAD MEMBER (POLONEZ COVE FORMATION, EARLY OLIGOCENE) AT KING GEORGE ISLAND, WEST ANTARCTICA: NEW INSIGHTS ON FACIES ANALYSIS, TAPHONOMY AND PALEOENVIRONMENTAL SIGNIFICANCE”, submetido ao periódico *Antarctic Science* (Anexo 3).

Os níveis de coquina do Membro Low Head, Formação Polonez Cove (Oligoceno inicial), Ilha Rei George, Antártica Ocidental, receberam aqui nova interpretação sedimentológica e tafonômica. A Formação Polonez Cove é altamente fossilífera e caracteriza-se pela presença de arenitos marinhos costeiros na base, seguidos por conglomerados e brechas, depositados em sistemas de fan-deltas. As coquinas, compostas principalmente pelo bivalve pectinídeo *Leoclunipecten gazdzickii*, ocorrem nos níveis mais basais da unidade e apresentam até três episódios de deposição bioclástica, associados a fluxos subaquosos por gravidade sob condições de alta energia. A acumulação das valvas nas proximidades dos locais onde os bivalves viviam provavelmente ocorreram em condições praias sob ação contínua de correntes de maré ou onda. O baixo grau de fragmentação e baixa variação de tamanho dos níveis coquinoides possivelmente resultaram da seleção por peneiramento em correntes de maré. Tal interpretação concorda com o cenário de progradação das porções frontais de fan-deltas que transportaram acumulações de conchas por curta distância e nas proximidades do sítio deposicional,

possivelmente entre o nível de base de onda de tempo bom e o nível de base de onda de tempestade.

5.2. Novo pectínídeo da Formação Destruction Bay (Oligoceno)

Resumo do artigo “A NEW FOSSIL *ADAMUSSIUM* (BIVALVIA: PECTINIDAE) FROM ANTARCTICA”, publicado no periódico *Polish Polar Research* (Anexo 4).

O presente trabalho apresenta a descrição taxonômica de nova espécie de pectínídeo do gênero *Adamussium* Thiele proveniente da Formação Destruction Bay (Oligoceno tardio), cujos afloramentos se encontram na região de Wrona Buttres, Ilha Rei George (Shetlands do Sul), Antártica Ocidental. O novo táxon contribui para o conhecimento paleontológico sobre os bivalves antárticos, além de auxiliar no entendimento do histórico pretérito do gênero, cujo representante moderno corresponde a uma espécie endêmica e de distribuição circum-antártica. O nome formalizado da nova espécie estará disponível após a publicação oficial no periódico.

5.3. Nuculídeos da Formação Cape Melville (Mioceno)

Resumo do artigo “NUCULIDAE (BIVALVIA) IN THE CAPE MELVILLE FORMATION, KING GEORGE ISLAND, ANTARCTICA, WITH AN OVERVIEW OF THE BIVALVE FAUNA”, publicado no periódico *Antarctic Science* (Anexo 5).

Este trabalho apresenta uma revisão dos bivalves nuculídeos da Formação Cape Melville (Mioceno inicial, Ilha Rei George). Dez táxons de bivalves foram registrados até o momento nas famílias Nuculidae (duas espécies), Sareptidae, Mallettiidae, Limopsidae (duas espécies), Limidae, Pectinidae, Hiatellidae, e Periplomatidae. Os Nuculidae incluem duas espécies de *Leionucula* Quenstedt, 1930. Uma delas, *L. melvilleana* n. sp., é descrita neste estudo e as demais consistem em duas espécies erigidas previamente por Anelli *et al.* (2006), que são por hora consideradas sinonímias atribuídas à espécie *Leionucula frigida* (Anelli, Rocha-Campos, Santos, Perinotto & Quaglio 2006). A assembleia, dominada por protobrânquios (89% dos exemplares), é uma fauna típica de substratos moles em ambiente costa-afora, com poucos exemplares de substratos duros transportados das proximidades. A análise do registro fóssil dos Nuculidae indica que a diversidade do grupo diminuiu na Antártica ao longo do Cenozoico.

5.4. Formação Cape Melville: novos táxons e paleobiogeografia

Resumo do artigo em preparação intitulado “BIVALVES FROM THE CAPE MELVILLE FORMATION (EARLY MIOCENE, WEST ANTARCTICA): NEW TAXA AND PALEOBIOGEOGRAPHY”, (Anexo 6).

A Formação Cape Melville, ricamente fossilífera, preserva um importante registro da história glacial cenozoica da Antártica. Até o momento, haviam sido descritos nove gêneros de moluscos bivalves desta unidade. O presente trabalho descreve três novos táxons de bivalves da Formação Cape Melville (*Limopsis* sp., *Limatula* sp. e *Periploma* (*Offadesma*) *antarctica* sp. nov.) e analisa a distribuição paleobiogeográfica dos gêneros da unidade ao do Cenozoico nas latitudes mais altas do Hemisfério Sul. Os bivalves de plataforma foram extintos das águas antárticas após o início do Mioceno ou início do Plioceno, o que discorda de cenários propostos previamente, nos quais as extinções teriam ocorrido ao longo do Cenozoico, relacionadas a todo o histórico de glaciação do continente. As extinções, na verdade, teriam ocorrido após a expansão da plataforma de gelo antártica, durante o evento glacial do Plio-Pleistoceno. Aqueles gêneros da Formação Cape Melville atualmente viventes na Antártica compreendem representantes euribáticos que não foram afetados pelo avanço do gelo plataformal durante o Neógeno, incluindo várias espécies recentes que ocorrem também nas áreas periféricas à Antártica.

5.5. Paleobiogeografia dos bivalves cenozoicos austrais

Resumo do artigo em preparação intitulado “BROKEN APART AND FROZEN OUT: FATE OF THE CENOZOIC SOUTHERN MARINE FAUNA”, (Anexo 7).

Utilizando os Bivalvia como táxon modelo, este estudo demonstrou que as províncias marinas biogeográficas atuais do Hemisfério Sul foram delineadas durante o Cenozoico, devido a uma combinação de fatores paleoambientais. As distintas províncias paleobiogeográficas originadas no início do Paleógeno se tornaram paulatinamente mais distintas após uma série de mudanças que incluem isolamento tectônico, formação da Corrente Circum-Antártica, além dos eventos associados de esfriamento climático e glaciação. As oscilações nos níveis de similaridade faunística entre as regiões mais austrais do Hemisfério Sul durante o Cenozoico apresentam significativa correlação com as tendências de temperatura global e ordem cronológica da fragmentação do Gondwana. A análise das curvas de similaridade de faunas e temperatura indica que o esfriamento aumentou o endemismo da fauna do Oceano Austral ao longo do Cenozoico. Esses

resultados apresentam implicações importantes para uma fauna marinha Antártica menos peculiar em um potencial futuro mais quente.

6. DISCUSSÃO INTEGRADA

Um dos grandes desafios da ciência antártica atual está relacionado à compreensão da evolução ambiental do Oceano Austral ao longo do Cenozoico (Barrett 2009). Dentro desse panorama, os moluscos bivalves representam um grupo adequado para o estudo das mudanças climáticas da Antártica, como aqui demonstrado, devido principalmente às características ecológicas, como aquelas delimitadas por temperatura e batimetria, capacidade de dispersão durante a fase larval (Scheltema 1977), além do potencial de preservação desses organismos no registro fóssil (ver anexo 7). Além disso, o entendimento de como os moluscos marinhos austrais responderam às mudanças ambientais cenozoicas é um tema central para a interpretação de mudanças climáticas futuras nos oceanos austrais e o consequente impacto sobre os ambientes marinhos.

Na Antártica, sobretudo na região peninsular, alguns depósitos preservando bivalves apresentam idades relacionadas aos principais eventos cenozoicos de glaciação, como as formações Polonez Cove e Melville (anexos 3-6). Embora os estudos taxonômicos sobre bivalves antárticos tenham sido realizados há mais de 40 anos (veja lista no anexo 2), trabalhos recentes, como os conduzidos nesta tese (anexos 4-6), revelaram que o conhecimento sobre a diversidade fossilífera cenozoica da Antártica é ainda incipiente e enviesado. No entanto, a reunião de extensas bases de dados alcança mais de 600 registros de espécies de bivalves antárticos descritos de depósitos cenozoicos (anexo 2). Esse registro, acrescido de dados provenientes de depósitos coetários de altas latitudes do Hemisfério Sul totaliza cerca de 41.000 registros, apresentando, portanto, grande potencial em estudos de distribuição paleobiogeográfica (anexos 6-7).

Uma inovação da presente tese foi a aplicação de métodos estatísticos e biogeográficos sobre o registro austral recuperado de bases de dados e literatura. Muito embora os métodos empregados (cluster e Análise de Parcimônia de Endemicidade, PAE) analisem os dados com base em similaridade, a PAE agrupa os clados por caracteres exclusivos, o que resulta em maior participação dos elementos endêmicos na definição dos clados. Esse é um método biogeográfico desenvolvido inicialmente para o estudo de dados paleontológicos de mesma idade (Rosen 1988). No entanto, o enfoque originalmente dado se materializou no uso dos dados de intervalos das diferentes áreas analisadas como unidades espaço-temporais distintas (Anexo 7). Com isso, a relação paleobiogeográfica dos gêneros de bivalves foi recuperada na análise também temporalmente, o que resolveu uma dificuldade intrínseca dos métodos biogeográficos desenvolvidos nos últimos anos.

A topologia de uma das árvores mais parcimoniosas da PAE evidenciou a presença de três grupos principais, resultado praticamente idêntico obtido pela análise de cluster. Os clados espaciais são compostos por áreas que compartilham táxons em diferentes intervalos de tempo, o que sugere que a fauna foi uniforme ao longo de um intervalo mais longo, em uma mesma área (grupo formado por intervalos mais antigos da Nova Zelândia, Figura 1 do Anexo 7). Os clados temporais agrupam áreas de um mesmo intervalo de tempo, indicando que áreas distintas foram parte da mesma província paleobiogeográfica ao longo de um intervalo de tempo restrito (grupo “antigo”, Figura 1 do Anexo 7). Tais clados aparecem com a mesma relação e as mesmas unidades áreas/intervalos em todas as topologias das árvores resultantes da PAE. Isto sugere que tais grupos são “monofiléticos” biogeograficamente e, portanto, apresentam topologias que potencialmente refletem um padrão paleobiogeográfico real. O terceiro tipo envolve clados mistos, que agrupam áreas distintas em intervalos de tempo também distintos. Estes clados resultam de áreas paleobiogeográficas instáveis que pertenceram a províncias distintas e maiores por intervalos mais curtos (como a Antártica e a América do Sul durante maior parte do Cenozoico, Figura 1 do Anexo 7).

Os resultados da presente tese confirmam a influência do histórico de mudanças ambientais ocorridos nas altas latitudes do Hemisfério Sul na fauna de bivalves marinhos austrais ao longo do Cenozoico (anexos 4-7). O resultado da influência ambiental se materializou na forma de eventos de dispersão, vicariância e extinção de determinados gêneros. O isolamento de alguns grupos marinhos aparece mais claramente com a quebra do Gondwana, enquanto eventos de vicariância aparecem após o primeiro evento de glaciação em larga escala na Antártica, após o Oligoceno (Anexo 7, mas ver também Anexo 6). A fragmentação de províncias paleogeográficas maiores em unidades menores se inicia, portanto, já no Oligoceno, com o surgimento de táxons aparentemente mais adaptados ao frio. No entanto, eventos de dispersão (*sensu* Lieberman & Eldredge 1996) parecem predominar no Paleógeno, enquanto os de vicariância parecem ser mais claramente evidentes no registro fóssil no Neógeno, com as glaciações atingindo a plataforma continental da Antártica. Como consequência, a formação da Frente Polar e a Corrente Circum-Antártica não parece, de acordo com o registro fóssil, isolar os táxons diretamente pela queda de temperatura, e sim, pela perda de determinados nichos ecológicos, como discutido no Anexo 6 (mas ver também resultados de Belanger *et al.* 2012 a partir de dados marinhos de regiões fora da Antártica). Nesse caso, o mais claramente observável na evolução do padrão paleobiogeográfico do registro de gêneros de bivalves é a restrição de

habitats costeiros e de águas rasas. Esse padrão pode potencialmente ser diferente para outros grupos marinhos e continentais.

Um aspecto importante é o fato de diversas evidências geoquímicas apontarem para pequenas oscilações de temperatura no quadro de esfriamento Cenozoico na Antártica (Zachos *et al.* 2001). Alguns intervalos parecem ter tido temperaturas mais amenas, seguidos de outros com expansão de geleiras e queda considerável de temperatura. Muito embora o fator restritivo para a sobrevivência dos grupos na Antártica pareça ser o avanço do gelo marinho, oscilações de temperatura no final do Neógeno e durante o Paleógeno poderiam ser consideradas indicativos diretos do avanço e retração dos mantos de gelo sobre a plataforma continental. Com isso, a dinâmica *dispersão X vicariância* de organismos marinhos da Antártica deve estar vinculada à dinâmica de temperatura inserida no quadro geral de esfriamento e avanço da plataforma de gelo. Intervalos de queda de temperatura pós-oligocênicos favoreceriam a especiação por vicariância, enquanto aqueles intervalos curtos, de temperaturas mais amenas, favoreceriam eventos de dispersão. Este cenário se enquadra no ‘modelo gerador de forma vicariante’ de Craw *et al.* (1999). Nesse caso, táxons de águas mais rasas estariam restritos em áreas subantárticas durante intervalos mais frios. Porém, os eventos de vicariância não podem ser observados diretamente com os métodos utilizados nos estudos realizados nesta tese. Para tanto, novos estudos realizados com base em panoramas de evolução filogenética poderiam explorar mais profundamente esse aspecto.

7. Conclusões

7.1. Tafonomia (Anexo 3)

- Níveis de coquina da Formação Polonez Cove (Oligoceno inicial) são compostos principalmente pelo bivalve pectínídeo *Leoclunipecten gazdzickii* e apresentam até três episódios de deposição, associados a fluxos subaquosos por gravidade sob condições de alta energia. A análise de fácies, no entanto, não sugere fluxos de tempestades como agente deposicional, como proposto previamente (Gaździcki 1984). A deposição teria ocorrido durante uma fase progradacional das porções frontais de fan-deltas que transportaram acumulações de conchas por curta distância e nas proximidades do sítio deposicional.

7.2. Taxonomia (Anexos 4-6)

- Os estudos taxonômicos dos bivalves provenientes das formações Cape Melville e Destruction Bay totalizam cinco novos registros, incluindo três espécies novas (*Leionucula melvilleana*, *Adamussium jonkersi*, *Limopsis* sp., *Limatula* sp. e *Periploma* (*Offadesma*) *antarctica*). Os novos dados contribuem para o conhecimento da diversidade Cenozoica do grupo na Antártica.

- O registro fóssil dos nukulídeos da Formação Cape Melville sugere que a família sofreu grande decréscimo de diversidade ao longo do Cenozoico, e novos estudos de cunho taxonômico e ecológico podem esclarecer qual agente relacionado ao histórico climático da Antártica determinou esse padrão.

7.3. Paleoecologia (Anexos 4 e 6)

- O registro fóssil da Família Pectinidae em depósitos antárticos indica maior diversidade do grupo durante o início do Mioceno. No entanto, várias espécies persistem no registro até o Plioceno, momento em que todos os representantes de águas rasas e hábito costeiro se extinguem, sendo que somente *Adamussium colbecki* persiste no Oceano Austral desde o Plioceno. Isso sugere que a maior pressão seletiva exercida sobre o grupo ocorreu por distribuição batimétrica, e não por estenotermia, como previamente sugerido. O avanço da plataforma de gelo durante o Plio-Pleistoceno restringiu a presença de ambientes mais rasos e, portanto, causou a extinção das espécies que ocupavam ambientes plataformais na Antártica.

- O Mioceno inicial representa um intervalo de tempo de temperaturas mais amenas na Antártica e regiões austrais, com diversos grupos (como os nukulídeos, limopsídeos e pectinídeos) alcançando alta riqueza e ampla distribuição.
- O registro austral dos gêneros da Formação Cape Melville em intervalos mais jovens sugere que apenas os representantes de preferências ecológicas em águas costeiras e rasas foram extintos das altas latitudes antárticas após o Plio-Pleistoceno, enquanto aqueles de ocorrência batimétrica mais ampla persistiram na Antártica. Isso sugere que os eventos de glaciação na Antártica baniram apenas os gêneros estenotópicos de águas rasas, devido à restrição de áreas costeiras e plataformais após o avanço da plataforma de gelo no Plio-Pleistoceno.

7.4. Paleobiogeografia (Anexos 4, 6 e 7)

- *Adamussium jonkersi*, registrado no Oligoceno final, representa, juntamente com *A. auristriatum*, do Oligoceno inicial, a linhagem do único pectinídeo vivente na Antártica, *A. colbecki*, cuja ancestralidade remonta o Oligoceno inicial.
- Os bivalves registrados na Formação Cape Melville representam linhagens austrais antigas, que remontam, pelo menos, o Cretáceo.
- Durante a deposição da Formação Cape Melville, no Mioceno inicial, os táxons registrados na unidade estavam amplamente distribuídos nas áreas austrais, sendo alguns deles cosmopolitas.
- A fauna de bivalves da Formação Cape Melville é representada, sobretudo, por protobrânquios, dos quais os nukulídeos são a família mais abundante. Estudos prévios apontam questões taxonômicas acerca da existência dos gêneros *Ennucula* e *Leionucula*. A distribuição austral aparentemente complementar de tais gêneros pode sugerir que ambos os gêneros se tratem de sinonímias, como anteriormente proposto.
- Análise multivariada e de parcimônia de todos os gêneros de bivalves registrados do Cretáceo ao Recente em regiões austrais sugere que a Província Weddelliana se fragmentou ainda no final do Cretáceo, e não no Eoceno como previamente proposto, a partir do isolamento faunístico ocorrido na Nova Zelândia. Tal fragmentação ocorreu principalmente por causas tectônicas.
- A definição das províncias austrais ocorreu ainda no Paleógeno. Austrália e sul da África do Sul se fragmentaram no Eoceno, mas permaneceram com algum compartilhamento de fauna até o presente.

- Antártica e sul da América do Sul compartilhavam gêneros ainda no Eoceno ou Oligoceno, formando uma província paleobiogeográfica única.
- Os eventos de glaciação ao longo do Neógeno intensificaram o padrão de distribuição heterogêneo dos gêneros de bivalves austrais alcançado no Paleógeno.

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Anexo 1

Mapas com as localidades citadas no texto e anexos.

ANEXO 1

Mapas com as localidades citadas no texto e anexos. **A**, Projeção azimutal equidistante do Pólo Sul, com as áreas abrangidas pela Convergência Antártica e adjacências; **B**, Extremidade da Península Antártica; **C**, Ilha Rei George; **D**, região entre o Cabo Vauréal e a Baía Rei George, Ilha Rei George; **E**, Península Melville, Ilha Rei George; **F**, região do Mar de Ross com as indicações das localidades detestemunhos; **G**, região de McMurdo Sound com as indicações das localidades de testemunhos. (Projeção cedida por J. P. Rodrigue, Universidade de Hofstra, Hempstead, Nova Iorque; compilação a partir de Zinsmeister 1982, Birkenmajer 2001, Troedson & Riding 2002, Prebble *et al.* 2006, Barrett 2009, Del Carlo *et al.* 2009, Paulsen & Wilson 2010).

1, Península Antártica	12, Victoria Land	23, Ilhas Sandwich do Sul	34, Ilha Greenwich	45, Península Melville
2, Ilhas Shetland do Sul	13, Mc Murdo Sound	24, Ilhas Okney do Sul	35, Ilha Livingston	46, Magda Nunatak
3, Cabo Norwegian	14, Montanhas Transantárticas	25, Ilhas Kerguelen	36, Ilha Deception	47, Penhasco Godwin
4, Baía Lutzow Holm	15, Montanhas Ellsworth	26, Baía Carnarvon	37, Arquipélago Palmer	48, Lions Rump
5, Baía Amundsen	16, Marie Byrd Land	27, Baía Otway	38, Ilha D'Urville	49, Battke Point
6, Baía Stefansson	17, Ilha Thurston	28, Passagem da Tasmânia	39, Ilha Joinville	50, Mazurek Point
7, Baía Prydz	18, Passagem de Drake	29, Platô Campbell	40, Ilha Dundee	51, Enseada Polonez
8, Montanhas Gamburtsev	19, Terra do Fogo	30, Ilhas Shetland do Sul	41, Ilha James Ross	52, Low Head
9, Baía Vincennes	20, Estreito de Magalhães	31, Ilha Rei George	42, Ilha Cockburn	53, Boy Point
10, Baía Commonwealth	21, Ilhas Falkland	32, Ilha Nelson	43, Ilha Seymour	54, Cabo Melville
11, Adelie Land	22, Ilhas Geórgia do Sul	33, Ilha Robert	44, Pico Vauréal	

Anexo 2

Espécies de bivalves fósseis provenientes de depósitos cretácicos
e cenozoicos da Antártica.

Anexo 2

Espécies de bivalves fósseis cretácicos e cenozoicos provenientes da Antártica.

Família	Espécie	Idade	Unidade	Ocorrência	Referência
Nuculidae	<i>Leionucula suboblonga</i>	Cretáceo Superior - Paleoceno	Fm. López de Bertodano e Fm. Sobral	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Leionucula hunickeni</i>	Paleoceno	Fm. Sobral	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Leionucula nova</i>	Eoceno	Fm. La Meseta	Ilha Seymour, Ilha Cockburn	Zinsmeister 1984, Stilwell & Zinsmeister 1987
	<i>Leionucula nova</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Leionucula</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Leionucula palmeri</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Leionucula melvilleana</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George	Whittle <i>et al.</i> 2012
	<i>Acila?</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Linucula? mcmurdoensis</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Pronucula</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Ennucula frigida</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anelli <i>et al.</i> 2006
	<i>Ennucula musculosa</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anelli <i>et al.</i> 2006
Nuculanidae	<i>Nuculana</i> sp.	Paleoceno inicial	Fm. Sobral	Ilha Seymour	Stilwell 2003
	<i>Nuculana</i> sp.	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Nuculana</i> cf. <i>oxyrhyncha</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Ledina</i> sp.	Paleoceno inicial	Fm. Sobral	Ilha Seymour	Stilwell 2003
	<i>Jupiteria</i> sp.	Paleoceno inicial	Fm. Sobral	Ilha Seymour	Stilwell 2003
	<i>Sacella eoantarctica</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Australoportlandia antarctica</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
Neilonellidae	<i>Pseudotindaria? levyi</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
Sareptidae	<i>Yoldiella</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
Yoldiidae	<i>Yoldia peninsularis</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anelli <i>et al.</i> 2006
	? <i>Yoldia</i> sp.	Mioceno inicial	ANDRILL-2A	Mar de Ross	Beu & Taviani 2013
	<i>Malletia</i> sp.	Cretáceo Superior	Fm. Snow Hill Island	Ilha Cockburn	Stilwell & Zinsmeister 1987, 2000
Malletiidae	<i>Australoneilo casei</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Australoneilo gracilis</i>	Paleoceno	Fm. Sobral	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Australoneilo rossi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984

	<i>Neilo beni</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Neilo rongelii</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anelli <i>et al.</i> 2006
Solemyidae	<i>Solemya rossiana</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Solemya peteri</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Solemya surolongata</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
Cucullaeidae	<i>Cuccullaea antarctica</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Cuccullaea elliot</i>	Paleoceno	Fm. Sobral	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Cuccullaea donaldi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Cuccullaea raea</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Cuccullaea</i> sp. cf. <i>C. raea</i>	Eoceno	Fm. La Meseta	Ilha Cockburn	Stilwell 2002
	<i>Cuccullaea</i> sp. cf. <i>C. donaldi</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Austrocuccullaea oliveroi</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Nordenskjöldia nordenskjöldi</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Arcidae	<i>Arca?</i> sp.	Eoceno	Fm. La Meseta	Ilha Cockburn	Stilwell & Zinsmeister 1987
Mytilidae	<i>Modiolus</i> cf. <i>M. pontotocensis</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Aulacomya anderssoni</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Aulacomya</i> sp. cf. <i>A. anderssoni</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Brachidontes sandalius</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Modiolus thomsoni</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Modiolus turneri</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Mytilus</i> cf. <i>magellanicus</i>	Oligoceno inicial	Fm. Polonez	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
Limopsidae	<i>Limopsis antarctica</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Limopsis</i> (<i>Limopsista?</i>) <i>antarctominuta</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Limopsis psimolis</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anelli <i>et al.</i> 2006
	<i>Limopsis infericola</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Whittle <i>et al.</i> 2011
	<i>Limopsis</i> sp.	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anexo 6
Bakevelliidae	<i>Phelopteria feldmanni</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Pulvinitidae	<i>Pulvinites antarctica</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Pinna</i> sp. cf. <i>P.</i>	Cretáceo Superior	Fm. Snow Hill Island	Ilha Cockburn	Stilwell & Zinsmeister 1987

Pinnidae	<i>anderssoni</i>				
	<i>Pinna freixeae</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Pinna sobrali</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Acesta shackletoni</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Acesta webbi</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Limidae	<i>Acesta (Antarcticesta) laticosta</i>	Eoceno	Fm. La Meseta	Ilha Cockburn	Stilwell & Zinsmeister 1987
	<i>Seymouritula antarctica</i>	Cretáceo Superior	Fm. López de Bertodano, Fm. Snow Hill Island	Ilha Seymour, Ilha Cockburn	Zinsmeister & Macellari 1988, Stilwell & Zinsmeister 1987
	<i>Limatula ferraziana</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Pico Vauréal)	Quaglio <i>et al.</i> 2008
	<i>Limatula</i> sp.	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anexo 6
	<i>Limatula</i> sp.	Pleistoceno	Bacia Victoria Land (Testemunho CRP-1)	Victoria Land	Taviani <i>et al.</i> 1998
Gyphaeidae	<i>Pycnodonte (Phygraea)</i> cf. <i>P. vesiculosa</i>	Cretáceo Superior	Fm. López de Bertodano, Fm. Snow Hill Island	Ilha Seymour, Ilha Cockburn	Zinsmeister & Macellari 1988, Stilwell & Zinsmeister 1987
	<i>Pycnodonte (Phygraea) seymourensis</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Ostrea antarctica</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
Ostreidae	<i>Ostrea seymourensis</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Ostrea</i> sp.	Eoceno	Fm. La Meseta	Ilha Cockburn	Stilwell & Zinsmeister 1987
	<i>Ostrea</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Crassostrea antarctogigantea</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Pecten</i> cf. <i>centralis</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
Pectinidae	<i>Eburneopecten</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Cyclopecten</i> cf. <i>C. guppyi</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Chlamys</i> sp.	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Stilwell 2002
	<i>Chlamys</i> sp.	Eoceno	Fm. La Meseta	Ilha Seymour, Ilha Cockburn	Zinsmeister 1984, Stilwell & Zinsmeister 1987
	<i>Chlamys</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Chlamys (Chlamys)</i> cf. <i>C. proximus</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Chlamys (Anatipoecten)</i> cf. <i>C. anatipes</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Chlamys (Swiftopecten)</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Austrochlamys</i>	Mioceno inicial	Bacia Victoria Land (Testemunho	Victoria Land (Mar de Ross)	Dell & Fleming 1975, Jonkers

	<i>marisrossensis</i>		CRP-1, ANDRILL-1B, 2A)		2003, Beu & Taviani 2013
	<i>Austrochlamys anderssoni</i>	Mioceno final – Plioceno final	Fm. Hobbs Glacier, Fm. Cockburn Island, Fm. Mendel, Fm. Sorsdal, Fm. Scallop Hill	Ilha James Ross, Ilha Cockburn, Ilha Black, Península Brown (McMurdo)	Jonkers 2003, Stilwell & Zinsmeister 1987, Beu & Taviani 2013
	<i>Austrochlamys heardensis</i>	Mioceno final	Fm. Drygalski	Ilha Heard	Jonkers 2003
	<i>Austrochlamys forticosta</i>	Mioceno final	Bacia Victoria Land (Testemunho ANDRILL-2A)	Victoria Land (Mar de Ross)	Taviani <i>et al.</i> 2010, Beu & Taviani 2013
	<i>Ruthipecten tuftensis</i>	Plioceno inicial	Fm. Sorsdal, Fm. Prospect	Vestfold Hills, Wright Valley (Victoria Land)	Beu 1985, Jonkers 2003, Beu & Taviani 2013
	<i>Ruthipecten</i> sp.	Plioceno inicial	Bacia Victoria Land (Testemunho ANDRILL-2A)	Mar de Ross	Beu & Taviani 2013
	<i>Leioclunipecten gaździckii</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984, Gaździcki & Studencka 1997, Jonkers 2003, Beu & Taviani 2013
Pectinidae	<i>Antarctipecten alanbeui</i>	Oligoceno – Mioceno inicial	Bacia Victoria Land (Testemunhos CIROS-1, CRP- 2/2A, ANDRILL-2A), Fm. Polonez Cove, Fm. Cape Melville	Victoria Land, Ilha Rei George (Lions Rump, Pico Vauréal, Península Melville)	Gaździcki & Pugaczewska 1984, Jonkers 2003, Quaglio <i>et al.</i> 2008, Beu & Taviani 2013
	<i>Adamussium auristriatum</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Pico Vauréal)	Quaglio <i>et al.</i> 2008
	<i>Adamussium jonkersi</i>	Oligoceno final, Mioceno inicial	Fm. Destruction Bay, Bacia Victoria Land (Testemunho ANDRILL-2A)	Ilha Rei George (Wrona Buttress), Mar de Ross	Stilwell <i>et al.</i> 2002, Anexo 4, Beu & Taviani 2013
	<i>Adamussium</i> n. sp. cf. <i>A. colbecki</i>	Mioceno inicial	Fm. Battye Glacier	Prince Charles Mountains (Baía Prydz)	Stilwell <i>et al.</i> 2002
	<i>Adamussium colbecki</i>	Plioceno final, Holoceno	Fm. Cockburn Island, Fm. Taylor	Ilha Cockburn, Minna Bluff (Mar de Ross)	Jonkers 1998, 2003, Stilwell & Zinsmeister 1987
Entoliidae	<i>Entolium seymourensis</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Entolium</i> sp.	Cretáceo Superior	Fm. Snow Hill Island	Ilha Cockburn	Stilwell & Zinsmeister 1987
	<i>Entolium sadleri</i>	Cretáceo Superior - Paleoceno	Fm. López de Bertodano e Fm. Sobral	Ilha Seymour	Zinsmeister & Macellari 1988
Trigoniidae	<i>Eselaevitrigonia regina</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Linotrigonia pygoscelium</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Cyamiidae	<i>Perrierina</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
Psammobiidae	<i>Gari (Psammobia) patagonica</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
Trapeziidae	<i>Trapezium</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
Corbulidae	<i>Corbula (Varicorbula)</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska

	<i>cf. hatcheri</i>				1984
	<i>Surobula nucleus</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Myidae	<i>Mya (Arenomya) nucleoides</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Mya (Arenomya) sowerbyi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Panopea</i> sp.	Cretáceo Superior	Fm. Snow Hill Island	Ilha Cockburn	Stilwell & Zinsmeister 1987
	<i>Panopea clausa</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Hiatella tenuis</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Hiatella harringtoni</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Panopea cf. P. philippii</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Panopea philippii</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Panopea</i> cf. <i>P. undatoides</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Panopea (Panopea) cf. P. regularis</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
Hiatellidae	<i>Panopea (Panopea) nucleoides</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Magda Nunatak)	Pugaczewska 1984
	<i>Panopea (Panopea) andreae</i>	Oligoceno final	Fm. Destruction Bay	Ilha Rei George (Wrona Buttress)	Studencka 1991
	<i>Panopea (Panopea) aff. P. worthingtoni</i>	Oligoceno final	Fm. Destruction Bay	Ilha Rei George (Wrona Buttress)	Studencka 1991
	<i>Panopea (Panopea) cf. P. regularis</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anelli <i>et al.</i> 2006
	<i>Hiatella cf. H. arctica</i>	Mioceno inicial	Bacia Victoria Land (Testemunho ANDRILL-2A)	Mar de Ross	Beu & Taviani 2013
	<i>Lucina scotti</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Lucina</i> sp.	Cretáceo Superior	Fm. Snow Hill Island	Ilha Cockburn	Stilwell & Zinsmeister 1987
Lucinidae	<i>Saxolucina sharmani</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Saxolucina sharmani</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Saxolucina</i> sp.	Paleoceno inicial	Fm. Sobral	Ilha Seymour	Stilwell 2003
	<i>Miltha?</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Cardita subrectangulata</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Cyclocardia</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Nemocardium</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
Carditidae	<i>(?Pratulium) minutum</i>				
	<i>?Arcturellina</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Pleuromeris</i> cf. <i>P.</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska

	<i>volckmanni</i>				1984
	<i>Eucrassatella wilckensi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Crassatella</i> sp.	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
Crassatellidae	<i>Eucrassatella (Spissatella)</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Eucrassatella (Eucrassatella)</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
Sportellidae	? <i>Anisodonta truncilla</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
Lahillidae	<i>Labillia larseni</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Labillia</i> sp.	Cretáceo Superior	Fm. Snow Hill Island	Ilha Cockburn	Stilwell & Zinsmeister 1987
	<i>Labillia huberi</i>	Paleoceno	Fm. Sobral	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Labillia wilckensi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
Astartidae	<i>Dozyia drygalskiana</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Thyasira townsendi</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Thyasiridae	<i>Thyasira</i> sp.	Paleoceno inicial	Fm. Sobral	Ilha Seymour	Stilwell 2003
	<i>Thyasira (Conchocele) australosulcata</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
Mactridae	<i>Mactra</i> cf. <i>M. irizari</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Mactra irizari</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Oxyperas (Pseudoxyperas) ortmanni</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
Gaimardiidae	<i>Gaimardia flemingi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	? <i>Costokidderia</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Venus (Ventricoloidea) newtoni</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump, Magda Nunatak)	Gaździcki & Pugaczewska 1984, Pugaczewska 1984
	<i>Timoclea</i> sp.	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Lions Rump)	Gaździcki & Pugaczewska 1984
	<i>Meretrix</i> cf. <i>iberingi</i>	Oligoceno inicial	Fm. Polonez Cove	Ilha Rei George (Magda Nunatak)	Pugaczewska 1984
Veneridae	<i>Eurhomalea florentinoi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Eurhomalea carlosi</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Eurhomalea inflata</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	" <i>Eurhomalea</i> " <i>claudiae</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Eurhomalea</i> cf. <i>antarctica</i>	Oligoceno final	Fm. Destruction Bay	Ilha Rei George (Wrona Buttress)	Studencka 1991
	<i>Eurhomalea</i> cf. <i>newtoni</i>	Oligoceno final	Fm. Destruction Bay	Ilha Rei George (Wrona Buttress)	Studencka 1991
	<i>Retrotapes andrillorum</i>	Mioceno inicial	Bacia Victoria Land (Testemunho)	Mar de Ross	Beu & Taviani 2013

ANDRILL-2A					
Veneridae	<i>Cyclorismina?</i> cf. <i>C. marwicki</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	? <i>Eumarcia</i> (<i>Atamarcia</i>) <i>robusta</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	? <i>Gomphina</i> <i>iheringi</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Cyclorismina marwicki</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Cockburnia lunulifera</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Marwickia woodburnei</i>	Paleoceno	Fm. Sobral	Ilha Seymour	Zinsmeister & Macellari 1988
	<i>Cyclorisma chanevi</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Pholadomyidae	<i>Goniomya hyriiformis</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Thraciidae	<i>Thracia askinae</i>	Cretáceo Superior	Fm. López de Bertodano	Ilha Seymour	Zinsmeister & Macellari 1988
Laternulidae	<i>Laternula elliptica</i>	Plioceno	Fm. Cockburn Island	Ilha Cockburn	Stilwell & Zinsmeister 1987
	? <i>Laternula</i> sp.	Mioceno inicial	Fm. Battye Glacier	Prince Charles Mountains (Baía Prydz)	Stilwell <i>et al.</i> 2002
Periplomatidae	<i>Periploma topei</i>	Eoceno	Fm. La Meseta	Ilha Seymour	Zinsmeister 1984
	<i>Periploma</i> sp.	Paleoceno inicial	Fm. Sobral	Ilha Seymour	Stilwell 2003
	<i>Periploma</i> cf. <i>P. topei</i>	Eoceno	Blocos erráticos	McMurdo Sound	Stilwell 2000
	<i>Periploma acuta</i>	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anelli <i>et al.</i> 2006
	<i>Periploma</i> (<i>Offadesma</i>) <i>antarctica</i> sp. nov.	Mioceno inicial	Fm. Cape Melville	Ilha Rei George (Península Melville)	Anexo 6

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**SHELL BEDS FROM THE LOW HEAD MEMBER (POLONEZ COVE
FORMATION, EARLY OLIGOCENE) AT KING GEORGE ISLAND, WEST
ANTARCTICA: NEW INSIGHTS ON FACIES ANALYSIS, TAPHONOMY AND
PALEOENVIRONMENTAL SIGNIFICANCE**

Abstract

Shell-bed levels occurring in the Low Head Member of the early Oligocene Polonez Cove Formation at King George Island, West Antarctica, are newly interpreted based on sedimentological and taphonomical aspects of the deposit. The highly fossiliferous Polonez Cove Formation is characterized by coastal marine sandstones, followed by conglomerates and breccias deposited in fan-delta systems. The shell-beds are composed mainly by the bivalve *Leoclinipecten gazdzickii* and occur at basal levels of the unit, showing up to three episodes of bioclastic deposition, associated to subaqueous gravity driven flows in high energy deposition. The shell accumulation in areas nearby the bivalve living site might have occurred in shoreface conditions under continuous action of tidal currents or waves. The low fragmentation rates and low size variation of the shell-bed layers would be resulted after selection by winnowing probably related to tidal currents. The interpretation fits to the scenario of a prograding fan-delta front transporting for short distance shell accumulations nearby the depositional site, possibly between fair-weather and storm wave bases.

Keywords: Polonez Cove Formation; Oligocene; shell-bed; sedimentology; taphonomy; pectinids, Antarctica.

1. Introduction

Shell-beds of “modern style” (*sensu* Kidwell 1990, Kidwell and Brenchley 1994, 1996) are bivalve-supported concentrations, usually generated under high energy events. These are internally complex, typically with sharp, erosional basal contact and discontinuous

grading (see Fürsich and Oschmann 1993, Li and Droser 1997, 1999, Simões *et al.* 2000). Such dense accumulations of bioclastic material are an important source of paleontological data and, frequently, the main only practical source of macroinvertebrate fossils in marine deposits (Simões and Kowalewski 1998). In Antarctica, this type of shell-beds (locally named “Pecten conglomerates”), are currently known from the Oligocene Polonez Cove Formation at King George Island and from the Pliocene Cockburn Island Formation, in the homonymous island (Gaździcki and Studencka 1997). The presence of shell-beds in these deposits was previously used to correlate both as Pliocene units (Andersson 1906, Adie 1962, Barton 1965, Fleming and Thomson 1979). However, isotopic dating and paleontological data from the type-area indicated a latest early Oligocene age (late Rupelian) for the shell-rich strata of the Polonez Cove Formation (Gaździcka and Gaździcki 1985, Birkenmajer and Gaździcki 1986, Gaździcki 1989, Birkenmajer *et al.* 1991, Dingle *et al.* 1997, Dingle and Lavelle 1998). Both deposits are essentially made up by pectinids, with the Polonez Cove Formation containing *Leoclinipecten gazdzickii* (Jonkers), while the Cockburn Island Formation is mainly composed by shells of *Austrochlamys anderssoni* (Henning) (Jonkers 2003, Beu and Taviani 2013).

The Polonez Cove Formation was firstly reported and named by Birkenmajer (1980, 1982, 1994), described in detail by Porębski and Gradziński (1987) and re-studied by Troedson and Smellie (2002). The shell-bed levels, as part of the Low Head Member, were described by Gaździcki (1984). However, some of the sedimentological and taphonomical signatures were overlooked, precluding the inclusion of key-data for the interpretation of the shell-bed genesis. Based on available studies, as well as new data collected in the type-section of the formation, we present herein new facies interpretation which partially corroborates previous works and introduce new details on the sedimentological and taphonomic history of the Low Head Member shell-bed accumulations.

2. Geological setting

The PCF crops almost laterally continuous in the Low Head area (Fig. 1, 2) as well-exposed rocks of Low Head, Siklawa and Oberek Cliff members (Porębski and Gradziński 1987, Troedson and Smellie 2002). The succession varies from 22 to 130m in thickness and comprises coastal marine sandstones, followed by conglomerates and breccias probably deposited in fan delta systems (Porębski and Gradziński 1987, Birkenmajer 2001, Troedson and Smellie 2002). The deposition was ice-influenced firstly during an extensive glaciation phase and later during deglaciation events, both strongly influenced by contemporaneous volcanic and tectonic activity related to the opening of the Bransfield Rift (Birkenmajer 1992, 1994, 2001). The unit is not intensely affected by tectonics and is limited both at the top and base by erosive discordances with the volcanic Mazurek Point/ Hennequin and Boy Point formations (Troedson and Smellie 2002). It comprises Krakowiak, Bayview, Low Head, Siklawa, Oberek Cliff and Chlamys Ledge members (Porębski and Gradziński 1987, Birkenmajer 2001, Troedson and Smellie 2002; **Table 1, Fig. 3**).

The overall PCF is considerably fossiliferous, and preserves different taxonomical groups, as calcareous nannofossils, bryozoans, ostracods, corals, bivalves, gastropods, brachiopods, foraminifers, worm ichnofossils, plant fragments and stromatolites (Gaździcki and Pugaczewska 1984, Birkenmajer *et al.* 1991, Birkenmajer 2001, Troedson and Smellie 2002, Gaździcki 2008, Quaglio *et al.* 2008). Fossil specimens are found mostly fragmented and sparsely distributed along the unit, except for the base of the Low Head Member at its type-area (Troedson and Smellie 2002), which contains relatively extensive and thick shell-beds – the subject of this work.

K-Ar dating from andesitic lavas at Lions Rump yielded 34.4 Ma as the maximum age of the Mazurek Point/ Hennequin Formation (Smellie *et al.* 1984). Various isotopic and geochronological studies indicate late early Oligocene as the age of the PCF. Isotopic Sr dating of brachiopod and bivalve shells collected from the base of the PCF (Krakowiak

Glacier Member) at Magda Nunatak yielded ages of 29.8 Ma (Dingle and Lavelle 1998), bivalves from shell beds at Low Head yielded 29.4 Ma (Dingle *et al.* 1997) and bivalves from Magda Nunatak yielded ages of 28.5 Ma (Dingle and Lavelle 1998).

3. Material and Methods

Four geologic sections were measured nearby the type-section of the PCF at Low Head locality, in the summer of 2005 during the 23rd Brazilian Antarctic Expedition. Facies analysis follows concepts by Walker and James (1992) and Miall (1996, 2000) of sedimentary facies description and identification of important stratigraphic surfaces.

Rock samples were collected from the shell-bed levels to analysis in the laboratory. The samples are housed at the Laboratory of Systematic Paleontology of the Institute of Geosciences, University of São Paulo, Brazil, Institute of Paleobiology of Warsaw, Poland, and at the Department of Biological Sciences, Faculty of Sciences, São Paulo State University, Bauru, Brazil.

Six samples from the basal level of coquinas were sectioned and polished for visualization of the biofabric (*sensu* Fürsich and Oschmann 1993) and sedimentary structures. Images of each sample were treated in drawing software to enhance black and white contrast between valves and matrix background (*i.e.*, matrix and cement). Bitmaps of each image were traced so each shell fragment or groups of fragments were considered as an object.

Other four samples were dismantled to removal of shells and valve measurement of the following taphonomic parameters: size (height), convexity (up or down), valve types (right or left), vertical orientation (parallel, concordant or oblique to the bedding) and horizontal orientation, or azimuth (north, northeast, east, southeast, south, southwest, west or northwest; see Kidwell *et al.*, 1986). The size (height and length) was measured according to the dorsal-ventral and anterior-posterior axes of the shell. The azimuths were measured in relation to the hydrodynamical stable position of the valves, which is the ventral-dorsal axis

indicating the direction and flow. In total, 340 shells were measured of three shell-bed layers. Although preserved in high number, specimens comprise easily breakable, very thin shells. Hence, it was not possible to measure all specimens for all parameters; hence the number of analyzed shells for each parameter is variable.

Yet, because middle layer is very thin and its pectinid specimens are densely packed and easily brittle, it was not possible to extract shell individuals in a proper number for statistical analyses. However, the lower (layer 1) and the upper (layer 2) concentrations yielded more than a hundred measurable specimens for the statistics (see appendix for taphonomic signatures and measurements). In order to check if the difference of each identified layers regarding the taphonomic parameters is significant, statistical analyses were performed in Bio Estat 5.3 and PAST using chi squared, contingency, as well as T and G tests, according to the kind of data to be analyzed.

4. Sedimentology of the Polonez Cove Formation at Low Head area

The facies association here described (**Table 2**, **Fig. 4**) indicates glacial terrigenous deposition with mainly volcanic influence, in shallow shelf conditions and partially corroborates the geological description by Troedson and Smellie (2002).

The base of the succession (Bayview Member; **Table 2**, **Fig. 4**) is characterized by centimetric intercalation of tabular beds of mudstones (**M**) and massive sandstones (**Sm**). The facies association suggests deposition by suspension and bottom currents related to high density hyperpycnal flows, possibly in prodeltaic or distal fan-delta systems, with glacial influence. This stratigraphic level is marked at the top by an erosive discontinuous surface. Troedson and Smellie (2002) suggest that this may be related to subaerial exposition due to a glacial eustatic rebound. However, we interpret this discontinuity as resulted from erosion by proximal gravity driven flows confined in subaqueous channels. This is based on the restricted

character of the erosional discordance showing highly sinuous contact and the massive presence of characteristic channel deposits in the Low Head Member.

At the base of the Low Head Member, matrix-supported massive conglomerates (**Cm**) and bioclast-supported conglomerates (**Cb**) occur as amalgamated decimeter-thick lenticular beds (**Table 2, Fig. 4**). The framework of the facies **Cb** is composed by marine macrofossils making up well sorted bivalve-dominated shell-beds with poorly sorted sandy matrix and occasionally pebble-sized clasts. The matrix and framework of the **Cb** facies show different granulometric selection degree, resulted from sporadic subaqueous high energy processes on a coastal fossiliferous deposit – the source of bivalve shells. Those processes are related to the input of an originally non-sorted gravitational flux that reworks and transports a granulometric selected fossiliferous accumulation. This facies is often separated by erosive surfaces and interbedded with unfossiliferous coarse and gravelly sandstones of the facies **Sp** (sandstone with parallel stratification), **Sr** (sandstone with climbing ripples), **Sm** (massive sandstone) and **Sl** (sandstone with low angle cross stratification), which are deposited by dense bottom fluxes associated with median to distal portion of fan-deltas. This facies association indicates a high energy episodic deposition of subaqueous gravity driven flows, associated to the prograding fan deltas fronts, between fair weather and storm wave bases. The absence of sedimentary facies reworked by wave orbitals or currents confirms the deposition in the offshore-shoreface transition.

The Siklawka Member is described as intercalations of fine to medium sandstones and mudstones, associated with rare gravelly sandstones which contain exotic clasts, supposedly deposited in offshore transitional condition with glacial influence (Troedson and Smellie 2002). In the studied sections there are no pelitic facies (**Table 2, Fig. 4**). Instead, a series of fine sandstones with planar stratification (**Sp**) interbedded with massive sandstones (**Sm**) is observed. Tabular beds of coarse sandstones fining upward, grading to fine sandstones with current ripples (**Sr**) occur occasionally. These beds suggest deposition by hyperpicinal influx

showing gradational flux deceleration towards the top, associated to distal portions of fan-deltas. This facies association indicates deposition in deeper waters than the Low Head Member facies, possibly in a distal fan-delta system below the storm wave base setting.

Metric beds of basaltic polymite breccias of the Oberek Cliff Member onlap these deposits in an erosive boundary, and are interpreted as deposited by subaqueous debris flows in shallow onshore waters (**Table 2, Fig. 4**). Numerous basaltic clasts, as well as pillow lavas and columnar disjunctions towards the top of the unit support the evidence of intense volcanic activity during the sedimentation (Porębski and Gradziński 1987).

Although the succession presents subtle thickening and fining upward pattern, it was not possible to confirm if the variation represents base level oscillations. The thickness and granulation differences along the beds may represent variations of the sedimentary input ratio or even lateral variations of the same fan-delta lobe.

5. Taphonomy

At outcrop scale, the shell-beds (facies **Cb**) are 5 to 40 cm thick concentrations at the base of the Low Head Member and show several meters of lateral extension, forming beds or flat lenses, with sharp and erosive basal contact (**Fig. 2**). They are internally complex, and at least three distinct concentrations are amalgamated in the thicker portions (**Fig. 2C**).

The material studied is mainly composed by complete valves of the thin-shelled pectinid *Leoclinipecten gazdzickii* (Jonkers) (Jonkers 2003, Beu and Taviani 2013), with very rare valve fragments. Externally, the shells are unabraded and only few of them are incrustated. Shell size varies from 2.4cm to 8.7cm in height and 2.1cm to 7.9 in length, with most valves varying from 4.6cm to 6.5cm (55.3% of height and 54% of length measurements), with maximum height of 6.5 cm, average of 5.3cm and maximum of 7.53 cm, except for one valve from layer 1 with 8.7cm height (see also Gaździcki 1984 and Jonkers 2003 for similar results). More rarely, other bioclasts include gastropods, other bivalve

mollusc shells, as well as bryozoans, echinoid and other unidentified invertebrate remains. Dense shell packing predominate at the base of each level, while disperse or loose packing are much common toward the top of the shell-rich interval.

The basal concentration, here named layer 1, is 20-30cm thick and show densely packed bioclasts in a poorly selected sandy matrix (**Fig. 2 C-D, Fig. 5**). The bioclasts comprise mostly 5.3cm average height pectinid valves, ranging from 4.6mm to 5.5mm (**Fig. 6A**), some of them disrupted (**Fig. 5**). More rarely additional clast types include other molluscs (as one found decimeter-sized hiatellid bivalve and very few centimeter to decimeter-sized gastropods), millimeter to centimeter echinoid and other unidentified invertebrate fragments, as well as rare granules and pebbles of volcanic origin that reach 4cm of diameter (**Fig. 5**). Pectinid shells are mostly disarticulate (7% articulate, n=212), convex-down (**Fig. 6B**) left valves (**Fig. 6C**), mostly horizontally oriented parallel to the bedding (**Fig. 6D**), and vertically oriented to S and W (**Fig. 6E**).

The transitional layer (middle) is very thin, often less than 4cm thick, and is composed by disarticulated (12.5% articulate, n=8), convex-down pectinid shells (75%, n=8), 56-66mm height, very densely nested and strongly imbricate (**Fig. 2 C-D**). The shells in this layer are hardly cemented to the rock matrix by carbonate cements, making their mechanical removal from the matrix very difficult or even impossible. The low sampling number (n=8) mars the statistical analysis of this layer. The middle layer is set apart from the basal layer by a very thin (5-10mm), unfossiliferous muddy bed of irregular surface.

The upper shell-bed concentration, here named layer 2, is 5 to 30cm thick and is characterized by bioclasts composed almost exclusively by pectinid shells that reach 5.1cm average height, most of them ranging from 4.6 to 5.5mm (**Fig. 2 C-D, Fig. 5A**). The shells are more sparsely packed if compared to layer 1 and middle layer and comprise preferentially disarticulated (10% articulate, n=120), convex-down (**Fig. 5B**) right valves (**Fig. 5C**), mostly perpendicular to the bedding (**Fig. 5D**) and showing SE as main umbonal direction (**Fig. 5E**).

At the top of thicker accumulations, layer 2 bears rare oblique articulated pairs (**Fig. 2C**).

Below this top level, the valves are only disarticulated and commonly nested. When nested, the shells are 10-20mm apart by the matrix. Very few specimens show incrustation by bryozoans (0.03%, n=120); when it occurs, the percentage of covered area is low (often below 10% coverage) and only externally at ventral margin. In cases of high incrustation percentage, the coverage may reach the central part of the disc or even dorsal margin of the shells.

Some of the studied taphonomic parameters are not distinct in layers 1 and 2 (as size, valve types and convexity), while others (as orientation and azimuth) are statistically distinct in both layers (**Fig. 6**). The size (height) frequencies of the specimens in layers 1 and 2 show similar height distributions (**Fig. 6A**), with no statistically significant difference of both layers (t test: dif. between means = -0.3030). Although both layers 1 and 2 yielded more convex-down shells, layer 1 is proportionally much richer in convex-up valves than layer 2 (**Fig. 6B**). The number of left valves in layer 1 is slightly greater than right valves, while layer 2 show the opposite: more right valves than left valves (**Fig. 6C**). However, this difference is not statistically significant ($\chi^2 = 0.288$; df. = 1), which means that both layers have the same proportion of left and right valves. Layer 1 contains highly different parallel, oblique and perpendicular valve numbers (**Fig. 6D**). Layer 2 shows the opposite distribution, with more perpendicular valves, followed by oblique and finally by parallel-oriented shells (**Fig. 6D**). The difference clearly observed in the histograms is statistically significant ($\chi^2 = 24.763$; df. = 2). The azimuth measurements in each layer are also different. Shells from layer 1 are mostly S and W oriented, while specimens from layer 2 show SE as main direction (**Fig. 6E**). This difference of main directions of layers 1 and 2 is statistically significant (G test = 47.7213; df. = 7).

6. Discussion

The material here analyzed includes three shell-bed levels (facies **Cb**) that correspond to different episodes of bioclastic deposition. Although the middle layer was not statistically analyzed due to low thickness and preserving characteristics that prevented us of proper sampling, the analysis of the upper and lower layers resulted in difference and similarity of taphonomical parameters.

The parameters that are not statistically different in both layers (valve size and type, **Fig. 6A and C**) are related to the bioclast source; in this case, the same for both layers. They were not resulted from selective transporting because of the low frequency of fragmented shells and the inferred sedimentological interpretation of high energy episodic deposition. All layers show low size variation of most valves and statistically equivalent numbers of left and right valves. This indicates that almost the same number of left and right, almost same-sized valves were present in the bioclast source. The same number of left and right valves might suggest that the original bioclast source would have been the same living site of the pectinids. However, the high frequency of almost same sized valves (4.6-5.5cm of both layers) and the low number of articulated valves (12.5% and 7.5%) suggest that the bioclast source was not a living pectinid community. Those features added to the low fragmentation require an agent of size sorting prior to the bioclast transport and final burial. The sedimentary process responsible for the in situ sorting of the shells is probably associated to winnowing, or other similar process, resulted from the action of tidal currents in shallow and protected waters. The shell accumulation in areas nearby the bivalve living site might have occurred in shoreface conditions possibly under continuous action of tidal currents or wave orbitals (**Fig. 7**). Bioclast accumulation in such environment is generally associated to low depth areas with current activity capable of transporting only finer grains, lagging the large clastic and bioclastic grains. This winnowing process selects bioclasts in variable size classes according to current intensity and, due to the lack of significant lateral transport, it tends to concentrate individuals with low or none fragmentation or mechanic abrasion. Also, the thin shell

material, the delicate external ornamentation, the absence or low degree of incrustation and the absence of abrasion of the pectinid bivalve shells indicate short residence time of the bioclasts in the Taphonomic Active Zone (Davies *et al.* 1989). All taphonomical signatures described in the shell-bed levels characterize parautochthonous assemblages (*sensu* Kidwell *et al.* 1986).

Following the biostratinomic phase of shell-bed genesis, the energy involved in the final depositional events of both layers was not substantially high in order to keep the thin, fragile ca. 5cm valves intact. Hence, the bioclasts underwent short, lateral transport in several episodes under relatively high energy conditions.

The studied samples suggest at least two, probably three, depositional events, resulting in different shell-bed layers. The variations in convexity and vertical orientation are statistically different in the two analyzed layers, as consequence of intensity and energy variation of the deposition flow. Because convex-down is a more stable position for shells to settle, higher proportion of shells in this attitude means that the flow energy was lower enough or lasting enough time during valve deposition. Layer 1 shows proportionally more convex-down valves, indicating that the pectinid bioclasts are more organized than those of layer 2. Conversely, layer 2 was deposited more rapidly than layer 1, as a result of a higher energy, short-term flow with faster sedimentation. This suggests that enough time elapsed until bioclasts attained their hydrodynamically stable position before the final burial of layer 1.

The azimuth measurements (**Fig. 6E**) indicate the most hydrodynamically stable position the pectinid specimens, and, thus, can be used in order to indicate gravity driven flow mean direction of the fan delta lobe. The fan-delta inflow into the basin is not unidirectional, so some variation in similar orientation quadrants is expected. Layer 1 indicates main flows towards south and west, while layer 2 indicates main flow to southeast. Layer 2 is expected to be deposited in higher energy conditions than layer 1, which explains the single main

direction of layer 2 and two main directions of layer 1, as consequence of different depositional events in each layer. Other less frequent azimuth measurements in layers 1 and 2 suggest slightly distinct flow directions, probably due to secondary currents. Both layers are expected to be in the same coastal line at the time of deposition (Troedson and Riding 2002). Hence, the azimuth orientations indicate the main direction of prograding fan-deltas and the direction of basin deposition. Generally, both layers indicate the quadrant south, which was the probable location of the basin depocenter in relation to the shoreline and final deposition site at the time of sedimentation. Small variations towards north and other directions, however, are due to erratic transport of some bioclasts, flow turbulence or even the presence of clasts blocking the bioclast flow. The presence of disrupted valves in layer 1 suggests that post-depositional compaction and soft deformation of water-saturated sediments affected only this level. This is supported by the presence of fluid escape and load-cast structures of finer sediments in those shell-bed portions. The massive feature of the **SM** facies confirms the action of fluidization associated with the sedimentary overload.

Although differences of both layers indicate occurrence of distinct depositional events, the process of deposition is similar. This interpretation fits to the scenario of a prograding fan delta front which transports for short distance shells that were accumulated nearby the depositional site, possibly between fair weather and storm wave bases (**Fig. 7**). Each layer of the shell bed is resulted from different deposition events of distinct lobes of the same fan-delta system.

Even though this hypothesis agrees well with a high energy scenario, it differs from the storm-wave deposition previously proposed (Gaździcki 1984, Porębski and Gradziński 1987). Tempestites are usually described as deposits generated by combined flows associated with unidirectional rip currents and oscillatory flow, commonly in shoreface and offshore settings under storm and hurricane events (see Aigner 1985, Walker and Plint 1992, Fürsich and Oschmann 1986, 1993, Clifton 2006). These combined flows result in particular

sedimentary structures, such as swaley and hummocky cross stratifications. Structures such these are commonly found in normally graded, fining upward successions that represent a decrease in flux energy and return to the day-by-day sedimentation. Shell-beds formed under these conditions typically show discontinuous grading, and stacked and nested shells (Fürsich and Oschmann 1986, 1993). Several features present in the Low Head Member shell-beds point to an episodic sedimentation under high energy conditions due to episodic input of fan-delta lobes. The features are the absence of storm-generated structures, the presence of channels with erosive base, small proportion of suspension facies (representing the background diary sedimentation), lateral extension of lenses and layers and the simultaneous transport of very coarse altogether with mud sediments with rare layers showing normal grading. Additionally, the discontinuous grading is not evident in the analyzed samples.

The presence of gutter casts (Whitaker 1973) at the base of some deposits associated with bivalve shell-beds were previously assigned as evidence of storm deposit (Porębski and Gradzinski 1987). Those sedimentary structures are recorded in different sedimentary environments as tidal flats, submarine fans (Whitaker 1973) and rivers (Smith 1985), and, thus, are non-conclusive as indicating storm-deposits. Gutter casts are formed by dragging particles along a base bed producing an object mark similar to a track. In a high energy gravitational flux of a fan delta front, in which transport of different granulometric class of sediments occurs, pebble clasts can be dragged at the bottom of substrate to form grooves similar to gutter casts. Our interpretation is corroborated by the facies association of the Low Head Member, which suggests deposition by subaqueous gravity driven flows under high energy conditions (Fig. 7).

7. Summary

The highly fossiliferous Low Head Member of the Polonez Cove Formation bears one of the thickest and best preserved 3D bivalve concentrations of Antarctica. The unit is mainly

composed by coastal marine sandstones, conglomerates and thin beds of finer grained facies deposited in fan delta systems, strongly influenced by glacial events and volcanic activity. The bioclastic facies preserves abundant pectinid bivalves of the species *Leoclinipecten gazdzickii* and, more rarely, other invertebrate remains, deposited by high energy episodic subaqueous gravity driven flows, associated to the prograding fan deltas fronts, between fair weather and storm wave bases. The shell-beds comprise at least three levels of accumulations that were size sorted by tidal currents or wave orbitals, previously to the depositional event, and probably nearby the bivalve living site. Once selected by winnowing in low-energy environment, shells of almost same size would undergo short, episodic, high energy transport until final burial by gravity driven flows of fan delta lobes (Fig. 7). Other high energy episodes would disarticulate once closed valves, which would be suspended and deposited in nestled, stacked or imbricate position. Successive episodes would erode and re-deposit other levels of coquina in different thickness, according to the amount of transported valves and flux intensity.

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TABLES

Table 1. Names and lithological characteristics of members of the Polonez Cove Formation.

Member	Lithology	Interpretation	Reference
Chlamys Ledge	conglomerate and gravelly sandstones with subordinate pelites	turbidites, debris flows and traction currents deposition under shallow marine environments with glacial influence	Troedson and Smellie 2002, Bitner <i>et al.</i> 2009
Oberek Cliff	basaltic lava flooding, lava breccias and subordinated sandstones and conglomerates	deposition under shallow glacial marine environment, influenced by volcanic activity	Birkenmajer 2001, Troedson and Smellie 2002
Siklawia	planar beds of sandstones, siltstones and claystones, intercalated with gravelly sandstones	turbidite currents deposition in the offshore transition zone	Birkenmajer 2001, Troedson and Smellie 2002
Low Head	fossiliferous basaltic conglomerates and sandstones	ice-sheet retreat influenced by volcanic activity	Birkenmajer 2001
Krakowiak Glacier	conglomerate and diamictite facies, with faceted and striated clasts	previous presence of ice sheets that would have transport lithic fragments westerly from the Transantarctic and Ellsworth Mountains	Birkenmajer 2001, Troedson and Smellie 2002

Table 2. Facies description and interpretation of the sedimentary processes of the Polonez Cove Formation at Low Head area.

Code	Facies	Description	Interpretation
Sm	sandstone, massive	medium to fine sandstones arranged in centimeter to decimeter planar beds of great lateral extension; locally normally graded	massive feature due to obliteration of previous structures by fluidization after sedimentary overload
Sl	sandstone, with low angle cross stratification	medium to fine sandstones arranged in decimeter beds with parallel stratification; locally, features of soft sediment deformation evidenced by load structures like pillow and flame	migration of bed forms over low angle beds at upper flowing regime
Sp	sandstone, with parallel stratification	discontinuous lenticular beds of matrix-supported massive conglomerate of Gray color, normally graded; matrix composed by medium to coarse poorly sorted sands	traction of bottom currents in planar beds at upper flowing regime
M	mudstone	beds of decimeter thickness of grey to brown massive sandstone; rare disperse granules	suspension deposits in low energy waters lacking action of bottom currents. The presence of granules is attributed to grain fall processes associated to the iceberg or ice floe melting
Cm	matrix-supported conglomerate, massive	discontinuous lenticular beds of matrix-supported massive conglomerates of gray color, normally graded; matrix composed by medium to coarse poorly sorted sands	subaqueous gravity driven flows
Cb	bioclast-supported conglomerate	decimeter to metric lenticular beds of bioclast-supported conglomerates, massive; matrix composed by medium to coarse poorly sorted sands; bioclasts comprise mainly disarticulated pectinid valves	subaqueous gravity drive flows that shortly transported pectinid valves
Sr	sandstone, with climbing ripples	medium to fine sandstones, arranged in planar decimeter beds with climbing ripples	subaqueous migrating dunes of irregular crests mainly under unidirectional currents in lower flow regime

FIGURES

Figure 1. Location maps of shell-beds from the Low Head Member, Polonez Cove Formation. **A**, Location of the King George Island in Antarctica. **B**, Exposures of the Polonez Cove Formation and other related units; arrow points to the area of studied sections and collected material (modified from Birkenmajer 2001 and Troedson and Smellie 2002).

Figure 2. Shell-beds of the Low Head Member, Polonez Cove Formation, at Low Head area, King George Island, West Antarctica. **A**, General view of the outcrop (BM, Bayview Member; LHM, Low Head Member; SM, Siklawka Member). **B**, Detail of the shell-bed. **C-D**, Samples of main shell-bed level of the Low Head Member, Polonez Cove Formation (Profile I of Gaździcki and Pugaczewska 1984), showing three shell-bed layers, including oblique valves in top of the layer 2, some of them articulated (arrows). (Samples housed at the Laboratory of the Institute of Geosciences, University of São Paulo, Brazil.)

Figure 3. Lithostratigraphical subdivision of the Polonez Cove Formation with indication of stratigraphic sections and shell-bed levels. Relation of thickness and chronology is not proportional. (Chart based on Birkenmajer 2001 and Troedson and Smellie 2002; Ages based on: a, Birkenmajer *et al.* 1989, K-Ar dating of andesitic lavas from Turret Point; b, Smellie *et al.* 1984, K-Ar dating of andesitic lavas from Lions Rump area; c, Dingle and Lavelle 1998, Sr isotopic dating of bivalve shells from the Krakowiak Glacier Member; d, Dingle *et al.* 1997, Sr isotopic dating of bivalve shells from Low Head, Polonez Cove and Lions Rump areas; e, Dingle and Lavelle 1998, Sr isotopic dating of bivalve and brachiopod shells from Magda Nunatak.)

← **Figure 4.** Stratigraphic sections of the Polonez Cove Formation measured at Low Head area, King George Island.

Figure 5. Bitmap-traced images of representative samples of shell-bed layer 1, Low Head Member, Polonez Cove Formation. Most bioclasts are oblique and convex-down oriented. Samples **A** and **B** are from the base of layer 1. (Sample A housed at the Laboratory of the Institute of Geosciences, University of São Paulo, Brazil; Samples B and C are kept in the collections of the Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland; Sample C is figured in Gaździcki 1984, fig. 5.)

← **Figure 6.** Taphonomic parameters of layers 1 and 2 of shell-bearing levels from the Low Head Member of the Polonez Cove Formation at Low Head area, King George Island, West Antarctica. **A**, histogram of shell size (height). **B**, histogram of shell convexity. **C**, histogram of valve types (left/ right). **D**, histogram of orientation in relation to the bedding. **E**, rosaceae diagram of pectinid azimuthal orientation.

Figure 7. Diagram showing deposition of pectinid shell-beds of the Polonez Cove Formation, King George Island.

Appendix

Taphonomical signatures of pectinid valves from the shell-bed levels of the Low Head Member, Polonez Cove Formation, King George Island, West Antarctica.

Layer	Sample number	Articulation	Valve		Height (mm)	Length (mm)	Position			Convexity		Azimuth
			Left	Right			Parallel	Oblique	Perpendicular	up	down	
LAYER 1	1	N	X			6,9	X			X	N	S
	2	N		X	7	6,4	X			X	N	S
	3	N	X		5,7	4,8	X			X	E	W
	4	N	X		4,7	4,8	X			X	NW	SE
	5	N	X		5,4	5	X			X	NE	SW
	6	N		X	5,1	5,1		X		X	N	S
	7	N	X		6,5	6,1	X			X	N	S
	8	N		X	5,5	5	X			X	NW	SE
	9	N	X		5,1	4,6		X		X	NE	SW
	10	N	X		5,1	4,6		X		X	E	W
	11	N		X	6,6	6,4	X			X	E	W
	12	N		X		5,7	X			X	E	W
	13	N	X			5,4	X			X	E	W
	14	N	X		5,9	6		X		X	E	W
	15	N	X		7,2	6,8	X			X	N	S
	16	N		X	6,5	6,6	X			X	NE	SW
	17	N		X	4,5	4		X		X	NW	SE
	18	N		X	5,2	5		X		X	NE	SW
	19	N		X	5,9		X			X	N	S
	20	N	X		6,3		X			X	N	S
	21	N	X					X		X	NW	SE
	22	N	X		2,5	2,4	X			X	NE	SW
	23	N	X				X			X	E	W
	24	N	X				X			X	NE	SW
	25	N	X				X			X	SE	NW
	26	N	X				X			X	SE	NW
	27	Y					X				E	W
	28	N	X		5	4,7	X			X	E	W
	29	N		X	4,5	4,7		X		X	NE	SW
	30	N	X		5,2	4,9	X			X	NW	SE
	31	N	X		4,8	4,3		X		X	E	W
	32	N	X		5,2	4,7	X			X	SE	NE
	33	N	X		5,2	4,7				X	E	W
	34	Y			3,7	6,1		X				
	35	N	X		5	4,9	X			X	NE	SW
	36	N	X		5	5,4	X			X	N	S
	37	N	X		5,5	5,2		X		X	NW	SE
	38	N	X		5,2	5,2		X		X	N	S
	39	N		X	6,1	5,4	X			X	N	S
	40	N		X	5	4,8		X		X	SE	NW
	41	N	X		5,4	4,9	X			X	N	S
	42	N	X		4,5	5,1		X		X	N	S
	43	N	X		5,3	5,1	X			X	E	W
	44	N		X				X		X	E	W
	45	Y			6,5	6,1	X				SW	NE
	46	N			5,5	4,9	X			X	E	W
	47	N	X		6,7	6		X		X	E	W
	48	N	X		6,6	6,1		X		X	N	S
	49	N	X				X			X	N	S
	50	N	X					X		X	N	S
	51	N		X	4,5		X			X	SE	NW
	52	N		X	5			X		X	S	N
	53	Y				6,2		X				
	54	N		X		5	X			X	L	W
	55	Y				4					NW	SE
	56	N		X	4			X		X	S	N
	57	Y			5,8		X				NW	SE
	58	Y									NW	SE
	59	Y										
	60	N		X	4					X	NW	SE
	61	Y			6,7					X	L	W
	62	N										
	63	Y				4,9				X		
	64	N	X		5,9	5,9				X		
	65	N		X	5,1					X		
	66	Y			3,5	3,8				X		
	67	N				5,3						
	68	N	X			4,3				X		
	69	N	X		3,9							
	70	N		X	6,4	6,4						
	71	N	X	X	5,8							
	72	N			6,6	3,2				X		
	73	N	X			6				X		
	74	N	X		2,7							
	75	N		X	2,4							
	76	Y	X			5,8				X		
	77	Y			5,9							
	78	N	X		5,4							
	79	N		X	5	4,5				X		
	80	N	X		4,3							
	81	Y			5,3					X		
	82	N		X	4,5	5,1				X		
	83	N			3,9							
	84	Y			5,4	5,3						
	85	N	X									
	86	N		X								
	87	N	X									
	88	N		X								
	89	N	X									
	90	N	X									
	91	N	X									
	92	N		X								
	93	N	X		5,4	5,6						
	94	N	X		4,6	5,2						
	95	N	X		4	4						
	96	N		X						X		
	97	N		X	5	4,8				X		
	98	N		X	6	5,8						
	99	N		X	5,1	5,1						
	100	N		X	4,8	5,6						
	101	N		X	5,6	6,3				X		
	102	N	X		6,3	6,9						
	103	N	X		8,7							
	104	N		X								
	105	N		X								
	106	N		X	5,8	5,1						
	107	N	X			5,9						
	108	N		X	5,7	5,2						
	109	N	X		6,3	6,8						
	110	N	X		5,4	6,2						
	111	N	X		4,9	5,7						
	112	N			5,2	5,2				X		
	113	N		X	5,9	5,8						
	114	N		X	5,2	5						
	115	N	X		4,1	4,1				X		
	116	N		X	4,7	5,3				X		
	117	N			5,3	5,5						
	118	N		X		7,9						
	119	N	X			4,2						
	120	N	X		5,5	5,4				X		
	121	N	X		4,8	5,3						
	122	N	X		5,1	4,6						
	123	N		X	6,5	3,3				X		
	124	N		X	6,3	6,4				X		
	125	N		X	5,4							
	126	N	X		4,2							
	127	N	X							X		
	128	N		X								
	129	N		X								
	130	N										
	131	N		X								
	132	N		X								
	133	Y										
	134	N	X		6,7	6,2				X		

	135	N		X	6,6	5,9		X		X	NE	SW
	136	N	X		5,6	5	X		X		NW	SE
	137	N		X	6,6	6,2		X	X		E	W
	138	N		X	5,4	5,1	X			X	SW	NE
	139	N		X	4,6	5				X	E	W
	140	Y			5,5	5		X				
	141	N		X	5,1	4,9	X		X		NE	SW
	142	N	X		6	5,5	X		X		N	S
	143	N		X	5,1	5,2		X	X		NW	SE
	144	N	X		5,5	5,2	X			X	N	S
	145	N		X	4,9	5,5		X	X		N	S
	146	N		X	5	4,9	X		X		SE	NW
	147	N		X	3,9	6,3	X		X		N	S
	148	N		X	5,3	4,8		X		X	N	S
	149	N	X		5,2	4,7	X			X	E	W
	150	N		X				X		X	E	W
	151	Y			6	6,1	X				SW	NE
	152	N	X		4,7	4,2	X		X		E	W
	153	N	X		5,1	5		X	X		E	W
	154	N	X		4,8	4,6		X	X		N	S
	155	N	X					X	X		N	S
	156	N	X					X	X		N	S
	157	N	X		5				X	SE	NW	
	158	N	X		4,4			X	X	S	N	
	159	Y				5,1		X				
	160	N	X			6,3	X		X		L	W
	161	Y				4,2	X				NW	SE
	162	N	X		3,8			X		X	S	N
	163	Y			5,5		X				NW	SE
	164	N					X				NW	SE
	165	N					X					
	166	N	X		2,5				X		NW	SE
	167	N	X		2,8				X		L	W
	168	N	X					X				
	169	N			5,8		X				SW	NE
	170	N	X		5,1	4,9	X		X		L	W
	171	N		X	5,7				X		N	S
	172	N			5,1	4,8	X		X		SW	NE
	173	N		X		5,3	X			X	N	S
	174	N		X		5,3		X		X	N	S
	175	N		X	4		X			X	SW	NE
	176	N		X	3,4	3,7			X		E	W
	177	N	X	X	5,2			X			N	S
	178	N			4,6	4,1	X				SW	NE
	179	N	X			5,6		X		X	N	S
	180	N			6,4							
	181	N		X	6							
	182	N		X		6	X		X		SW	NE
	183	N			5				X		SW	NE
	184	N			6,8			X			N	S
	185	N			6,4	6,5	X			X	SE	NW
	186	N			3,9		X			X	N	S
	187	Y			5,9		X				SE	NW
	188	N		X	7,1	6,9	X		X		SE	NW
	189	N			4		X		X		SE	NW
	190	Y			5,8	6	X				SE	NW
	191	N					X			X		
	192	N					X			X		
	193	N					X			X		
	194	N					X			X		
	195	N					X			X		
	196	N					X			X		
	197	N					X			X		
	198	N					X			X		
	199	N	X		6,7	6,5		X				
	200	N	X		5,2	4,7	X					
	201	N			5	4,5		X				
	202	N		X			X					
	203	N		X	5,6	5,1		X		X		
	204	N			6,6	6,2	X			X		
	205	N		X	5	5	X			X		
	206	N		X	5,3	4,9	X			X		
	207	N		X	4,8	4,9		X		X		
	208	N			5,6	4,7	X		X			
	209	N	X		5,7					X		
	210	N		X			X			X		
	211	N					X			X		
	212	N			6	5,9	X			X		
MIDDLE LAYER	213	Y			6	5,8	X		X		N	S
	214	N		X	6,6			X		X	N	S
	215	N		X	5,9				X		E	W
	216	N		X	5,6		X			X	NE	SW
	217	N			5,7	5,5	X		X		E	W
	218	N	X		5,7		X		X		NE	SW

LAYER 2	219	N		X	6	6		X			X	NE	SW	
	220	N		X	6,4			X			X	N	S	
	221	N		X	6,4	7			X		X	NW	SE	
	222	N	X		4,7	5			X		X	NW	SE	
	223	N		X	6	6,3			X		X	NW	SE	
	224	N		X	6,4	5,9			X	X		NW	SE	
	225	N	X			2,1		X				NW	SE	
	226	N		X	5,2	4			X			NW	SE	
	227	N	X		6,3	6,3			X			NW	SE	
	228	N		X	2,5	2,4			X			NW	SE	
	229	N	X		5,8	6,1			X			NW	SE	
	230	N	X		3,2	3,3			X			NW	SE	
	231	N		X	5,4	4,9			X			NW	SE	
	232	Y			6	6,3			X			NW	SE	
	233	N	X		4,4	6			X			W	E	
	234	N		X		4,8			X		X	N	S	
	235	N		X		4,9		X			X	X	W	E
	236	N	X		4,1	4,9		X			X		N	S
	237	N	X		6,8	7,2		X					N	S
	238	N	X		3,5	3,3						X		
	239	N	X		5,5	5,7				X		X	NW	SE
	240	N		X						X		X	W	E
	241	N	X		5,3	5			X			X	NE	SW
	242	N	X		4,2	5			X			X	NE	SW
	243	N	X			2,8		X					N	S
	244	N		X	5,4	5			X		X		NW	SE
	245	N	X		5	5,6			X			X	W	E
	246	N		X	5,1	5,1			X			X	W	E
	247	Y			6,4	5,9			X			X	SW	NE
	248	N		X	5				X			X	SW	NE
	249	N		X	6,4	6,2			X			X	NW	SE
	250	Y			5,8	6,1		X					NW	SE
	251	N		X		5,7		X				X	NE	SW
	252	N		X		5,7		X				X	SW	NE
	253	N	X		5,4	5,5			X			X	N	S
	254	N	X			4,4		X			X		N	S
	255	N	X		5,7			X				X	SW	NE
	256	N	X			4,9				X			SW	NE
	257	Y			5,3	5,2			X				SE	NW
	258	N	X		4,5	4,9			X			X		
	259	N	X		4,7					X			E	W
	260	N	X		4,8	4,8				X			E	W
	261	Y			4,4				X				SE	NW
	262	N	X		6,1				X		X		SE	NW
	263	N	X			5,9				X			E	W
	264	N		X		4,5				X			SE	NW
	265	N	X			5				X			E	W
	266	N		X	4,8	4,8			X		X		NW	SE
	267	N	X			4,8			X		X		E	W
	268	N		X	5,5				X			X	N	S
	269	N	X		4,9				X		X		NE	SW
	270	Y			5				X				N	S
271	N		X	4,9	4,8			X			X			
272	N	X		2,5	2,3				X		X			
273	N		X	2,7	4,5		X				X			
274	N	X		5,4	3,2		X				X			
275	N	X		5,6	4,9				X	X				
276	N		X	4	4				X	X				
277	N	X		4,5	5,1				X	X				
278	N	X		4,3	4,2				X	X				
279	N	X		6	6,4				X	X				
280	N	X		4,5	6				X	X				
281	N		X	4,9	4,8				X	X		NW	SE	
282	N	X		2,4	2,4				X		X	NW	SE	
283	N		X	6,5	7,1				X		X	NW	SE	
284	Y			4,9	4,7				X			NW	SE	
285	N	X		3	2,1			X				NW	SE	
286	N		X	5	5				X		X	W	E	
287	N	X		5,3	4,9		X					N	S	
288	N		X		2,2				X			NW	SE	
289	N	X		5	5,5				X			NW	SE	
290	N		X	5	5				X			NW	SE	
291	N	X		5,7	6				X			NW	SE	
292	N		X	5,9	6				X			NW	SE	
293	N	X		4,8	4,8				X			NW	SE	
294	N	X		5,3	5				X			SW	NE	
295	N		X	6,6	7				X			W	E	
296	N		X	5,1	5				X		X	N	S	
297	N		X	3,1	2,9		X			X	X	W	E	
298	N	X		4,5	4,8		X			X		N	S	
299	N	X		4,8	5,1			X			X	N	S	
300	N	X		4,9	5,5						X			
301	N	X		4,9	5,5				X		X	NW	SE	
302	N		X	6,1	6,4				X		X	NW	SE	

303	N	X	6,1	6,3	X		X	NE	SW
304	N		X	4,9	5,2	X	X	NE	SW
305	N		X	5,3	4,1	X		N	S
306	N		X	5,3	4,1	X	X	NW	SE
307	N		X	4,2	5,8	X	X	W	E
308	N		X	4,5	5,9	X	X	W	E
309	Y			4,2	4,9	X	X	SW	NE
310	N		X	5	5,5	X	X	SW	NE
311	N		X	4,3	5,1	X	X	NW	SE
312	Y			5	4,7	X		NW	SE
313	N		X	5	5,1	X	X	NE	SW
314	N		X	5	4,7	X	X	SW	NE
315	Y			5,5	5,4	X		SE	NW
316	N		X	5,3	5,5	X	X	N	S
317	N	X		5,4	3,7	X	X	SW	NE
318	N		X	5,3	4,9		X	SE	NW
319	N		X	5,3	4,5	X	X	NE	SW
320	N	X		5,5	5,3	X	X		
321	Y			6		X		SE	NW
322	N		X	5,4	5	X	X		
323	N		X	4,9			X	E	W
324	N	X		2,9	2,9		X	E	W
325	Y			4,6		X		N	S
326	N		X	6,2		X	X	SE	NW
327	N		X		5,8		X	E	W
328	N		X	4,9			X	X	
329	N	X			4,7		X	E	W
330	N		X	5,1	5	X	X	NW	SE
331	N		X		4,9	X	X	E	W
332	N		X	4,3		X		N	S
333	N		X	5,2	5,2		X	X	
334	N		X	5	5		X	X	
335	N		X	6,2	6,4		X	X	
336	N	X		6,3	6,1		X		X
337	N	X		5,5	5,6		X	X	
338	N	X		5	5,1	X		X	
339	N		X	6,3	6	X		X	
340	N		X	6,3	5,9		X	X	

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A new fossil *Adamussium* (Bivalvia: Pectinidae) from Antarctica

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Abstract: *Adamussium jonkersi* sp. nov. is described from the Late Oligocene Destruction Bay Formation, Wrona Buttress area, King George Island (South Shetlands), West Antarctica. The unit, characterized by volcanic sandstone, is a shallow marine succession deposited in a moderate- to high-energy environment. The thin-shelled pectinids, collected from the lower part of the unit, are preserved mostly as complete valves. Shell thickness, sculpture pattern and umbonal angle suggest a free-living, inactive swimming life habit.

Key words: Antarctica, *Adamussium*, Pectinidae, Destruction Bay Formation, Oligocene.

Introduction

Species of the pectinid genus *Adamussium* are recorded from the latest Early Oligocene onwards (Jonkers 2003; Quaglio *et al.* 2008). The living member of the genus, the circum-Antarctic species *Adamussium colbecki* (Smith, 1902), was the subject of several studies focusing on its geographical distribution (Schiaparelli and Linse 2006), systematics (Barucca *et al.* 2005), ecology (Stockton 1984), physiology (Chiantore *et al.* 2003; Heilmayer *et al.* 2005) and environmental analysis (Corsi *et al.* 2004; Caroli and Bottoni 2010).

Currently, four species of *Adamussium* are known, all restricted to Antarctica. Here we describe a new species from the middle Late Oligocene Destruction Bay Formation, cropping out at Wrona Buttress, King George Island (KGI).

Background

Four species attributed to the genus *Adamussium* have been identified so far from Cenozoic deposits and Recent records from Antarctica. The species *A. alanbeui* Jonkers, 2003 and *A. auristriatum* Quaglio *et al.* 2008, from Oligocene to Early Miocene rocks, are the oldest known species of this genus (Jonkers 2003; Quaglio *et al.* 2008). Specimens of *A. alanbeui* and *A. auristriatum* were collected from CIROS-1 and CRP-2/2A drill-cores, Ross Sea, with additional specimens recorded in deposits of the Polonez Cove Formation, Lions Rump area, and the Cape Melville Formation, Melville Peninsula, both at KGI (Jonkers 2003; Quaglio *et al.* 2008). The second-oldest species, *A. auristriatum*, is recorded from the Early Oligocene Polonez Cove Formation, Vauréal Peak area, KGI (Quaglio *et al.* 2008). Much younger are *A. colbecki cockburnensis* Jonkers, 2003, found in the Late Pliocene Cockburn Island Formation, cropping out at the homonymous island, and *A. c. colbecki*, identified from the Late Pliocene to Early Pleistocene cores of CRP-1, James Ross Island and from Recent records around Antarctica (Jonkers 2003). The time ranges of all *Adamussium* species are shown in Fig. 1.

Fig. 1. Stratigraphic ranges of *Adamussium* species (data from Jonkers 2003 and Quaglio *et al.* 2008).

Material and methods

Geological setting.—The most extensive outcrops of the Destruction Bay Formation (DBF) occur in coastal cliffs to the northwest of Melville Peninsula (KGI, South Shetlands), named Wrona Buttress, where the unit reaches 90 m (Troedson and Riding 2002) to 100 m thick (Birkenmajer 1987) (Figs 2A, B; 3). Other exposures are found at the northern and southern edges of Cape Melville (Troedson and Riding 2002) (Fig. 2B). The DBF is the middle unit of the Moby Dick Group (see Fig. 2C), which also includes the lower Sherratt Bay Formation (olivine-augite basalt lavas) and the upper Cape Melville Formation (fossiliferous

Fig. 2. Location maps of the Destruction Bay Formation and other related units. **A.** Melville Peninsula and vicinity, King George Island, West Antarctica. **B.** Destruction Bay Formation and other units of the Moby Dick Group. **C.** Subdivision of the Moby Dick Group (from Birkenmajer 1982).

Fig. 3. Wrona Butte. Exposure of the horizontally bedded Destruction Bay Formation, which the pectinids were collected from (arrowed). Photograph by A. Gaździcki, January 1981.

marine shale, siltstone and fine sandstone) (Birkenmajer 1982, 2001; Birkenmajer *et al.* 1983; Troedson and Riding 2002). The DBF consists of pale gray to brown sub-horizontal volcanic sandstone, fine to medium and medium to coarse-grained, with occasional muddy and gravelly sandstone beds, tabular to channelized, displaying tabular to trough cross-bedding, with parallel and cross laminations (Troedson and Riding 2002).

Fossils occur throughout the unit, except in the uppermost subunit (Troedson and Riding 2002), and are more common in the bottom to the middle part of the unit (Birkenmajer 1982, 1987). Fossils include brachiopods (Biernat *et al.* 1985), foraminifers (Birkenmajer and Łuczkowska 1987), molluscs (belemnites, Birkenmajer *et al.* 1987; bivalves, Studencka 1991; gastropods, Birkenmajer 1982, 1987; Troedson and Riding 2002), cnidarians (solitary corals, Roniewicz and Morycowa 1987), as well as fish and wood fragments (Birkenmajer 1982, 1987; Troedson and Riding 2002; see also Beu 2009).

The pectinid species here described was collected from the lower part of the unit (Fig. 3), ranging from subunits 1 to 2 of Troedson and Riding (2002).

The Moby Dick Group records a glacial event in West Antarctica, with the DBF being an interglacial phase, followed by the glacial deposits of the Cape Melville Formation (Birkenmajer 1987). The DBF, dated as Late Oligocene (25.3 ± 0.8 Ma; Dingle and Lavelle 1998), is interpreted as a shallow marine succession originating from the reworking of basaltic lavas and tuffs of the underlying

Sherratt Bay Formation (Birkenmajer 1982). The basal subunits were deposited in a moderate-energy environment and the upper subunits were deposited in a high-energy environment, with a shallowing-upward tendency showing possible prograding architecture (Troedson and Riding 2002).

Fossil collection. — The studied shells were collected by A. Gaździcki during the 5th Polish Antarctic Expedition to Artowski Station (1980/1981) and by M. Lavelle and D. Hornby in February 1996. The material includes eleven specimens with thin recrystallized shells, some of them are partial internal and external moulds with some preserved shell material. All examined specimens are still retained in the rock matrix. The specimens are housed in the collections of the Institute of Paleobiology PAS in Warsaw, Poland, under catalogue number ZPAL/L3/38–42, and the British Antarctic Survey (BAS) in Cambridge, United Kingdom, under number P.2904.10.1.

Measurements and classification. — Specimens were measured with reference to the hinge line. The length, height and width are in relation to the greatest measured lines parallel, perpendicular and orthogonal to the hinge line, respectively. Elongation and obesity indexes were calculated according to Stanley (1970). Abbreviations in tables are as follows: AA, length of the anterior auricle; E, elongation; H, height; L, length; LV, left valve; O, obesity; OL, length of the outer ligament; RN, rib number; RV, right valve; UA, umbonal angle; W, width.

Pectinid specimens from Wrona Buttress have some of the diagnostic characters of the genus *Adamussium* proposed by Jonkers (2003, p. 67). The characters include: extremely thin shells with low costae formed by simple crenulation of the disc, a straight hinge, and commarginal lirae.

Systematic paleontology

Family Pectinidae Rafinesque, 1815

Genus *Adamussium* Thiele, 1934

Type species: *Pecten colbecki* Smith, 1902; holotype: a right valve collected from 18 m depth off Franklin Island, Ross Sea, Antarctica, during the "Southern Cross" Expedition; Natural History Museum, London, number 1902.5.16.147 (Jonkers 2003).

Adamussium jonkersi sp. nov.

(Figs 4–6, Table 1)

Etymology: After H.A. Jonkers, for his noteworthy contribution to the paleontological studies of pectinids of the Southern Ocean.

Material. — Holotype, right valve (L3/41). Paratypes, right valves (L3/38, 40, P.2904.10.1) and left valves (L3/39, 42).

Diagnosis. — Radial sculpture of 7–9 broadly undulating, well-developed main plicae, intercalated with faintly developed secondary plicae on the ventral

Fig. 4. *Adamussium jonkersi* sp. nov., shell bed: hand sample with paratype ZPAL/L3/40 (arrowed at center) and holotype ZPAL/L3/41 (arrowed at top left). Image by G. Dziewińska and M. Dziewiński.

part of the disc of most specimens; commarginal sculpture of distinct but weak lirae, with groups almost equally and closely spaced down the entire shell; RV anterior auricle rounded, with 3–4 radial costae observed internally.

Description. — Shell moderate to small in size, suborbicular (chlamydoid to aequipectinoid); dorsal margin short, ventral margin wide and rounded; equant; apparently very compressed, with moderately convex valves, LV more convex than RV; beaks orthogyrate; umbonal angle narrow (*ca* 110°); radial sculpture of 7–9 broadly undulating, well-developed main plicae, intercalated with faintly developed secondary plicae towards ventral part of disc; commarginal sculpture of distinct but weak lirae, in groups almost equally and closely spaced down entire shell; hinge line straight; RV auricles apparently asymmetrical, anterior auricle rounded, with 3–4 radial costae observed internally.

Table 1

Measurements of representative specimens of *Adamussium jonkersi* sp. nov.
(* specimen incomplete)

Specimen	Valve	H	L	W	E	O	OL	AA	UA	RN
ZPAL/ L3/ 40	RV	40.8	38.4	11*	0.94	3.71	24.5	11.5	110°	9
ZPAL/L3/ 41	RV	49.5*	53.5	6.8*	1.08	7.28	–	–	–	9
P.2904.10.1	RV	49.8	44.2	–	0.89	–	–	–	100°	8

Table 2

Comparative features of *Adamussium colbecki colbecki*, *A. c. cockburnensis*, *A. alanbeui*, *A. auristriatum* and *A. jonkersi* sp. nov. (¹ according to Jonkers 2003; ² according to Quaglio *et al.* 2008; ³ specimens from Destruction Bay Formation at Wrona Buttress; – not observable).

Features	<i>Adamussium c. colbecki</i> ¹	<i>Adamussium c. cockburnensis</i> ¹	<i>Adamussium alanbeui</i> ¹	<i>Adamussium auristriatum</i> ²	<i>Adamussium jonkersi</i> ³
Size	moderate (mean H = 70 mm)	moderate (mean H = 56 mm)	small (mean H < 50 mm)	moderate (mean H = 52)	small (mean H = 45 mm)
Valves	slightly opisthocline (AVH/PVH = 0.96)	opisthocline (AVH/PVH = 0.91)	acline	procline (AVH/PVH = 1.19)	apparently procline
Convexity	moderate	weak	weak	moderate	weak
Greater convexity	LV	LV	LV	RV	LV
Umbonal angle	very wide (138°)	wide (134°)	narrow (110°–120°)	wide (130°)	narrow (110°)
Radial sculpture	20 broadly undulating with intercalated low plicae	15 broadly undulating with intercalated low plicae	none	10–15 main plicae with intercalated low plicae	7–9 broadly undulating main plicae with intercalated low plicae at ventral margin
Com-marginal sculpture	distinct lirae with groups differently spaced	lirae regularly and widely spaced	none	lirae, weakly marked, regularly and widely spaced	distinct but weakly marked lirae, with groups almost equally and closely spaced
Micro-sculpture	wide to narrow antimarginal ridges	narrow antimarginal ridges	narrow antimarginal ridgelets	narrow antimarginal ridgelets	–
Auricles symmetry	highly symmetrical (AOL/POL = 1.02)	highly asymmetrical (AOL/POL = 1.4)	slightly asymmetrical (AOL/POL = 1.1–1.3)	highly symmetrical (AOL/POL = 1.01–1.08)	apparently asymmetrical
Auricles sculpture	none	none	none	anterior auricle with radial costae	anterior auricle with radial costae observable internally
Byssal notch	very deep (arcuate or acute)	deep	very shallow	very deep (acute)	–
Number of byssal teeth	very variable (mean = 2.5)	–	–	6	–

Comparison. — The characters of all known *Adamussium* species are summarized in Table 2. Assessing all of the characters, each species is unique, however, not many of the characters on their own indicate a clear taxonomic affinity between any two taxa. This can be seen from Table 2, where one species seems to be more related to another considering a given character (*e.g.* the similar opisthocline shape of the valves in *A. c. colbecki* and *A. c. cockburnensis*) and to a different species if another character is considered (*e.g.* the moderate convexity of the valves and symmetrical auricles in *A. c. colbecki* and *A. auristriatum*). Finally, *A. auristriatum* and *A. jonkersi* sp. nov. are similar in possessing procline valves and striated auricles. *A. alanbeui* differs from all other species by lacking radial plicae. Apart from this, Table 2 also shows that only *A. c. colbecki* and *A. jonkersi* sp. nov.

Fig. 5. *Adamussium jonkersi* sp. nov. **A–B.** External view of RV (paratype P.2904.10.1). **C–D.** Polymer clay cast of external mold of RV (holotype ZPAL/L3/41). **E.** Internal mould of LV (paratype ZPAL/L3/39). **F–G.** Polymer clay cast of external mold of RV; lower left hand side of shell only partially preserved (paratype ZPAL/L3/40). **H.** Camera lucida drawing of **G**. Scale bars 5 mm. Images of **A–B** by C. Gilbert; **C, D, F, G** by L.E. Anelli and F. Quaglio; **E** by G. Dziwińska and M. Dziwiński.

Fig. 6. Paratype ZPAL/L3/40, commarginal lirae in SEM micrographs of ventral margin of shell (umbo to the top left). Scale bars 500 μ m.

are morphologically distinct. Therefore, the small morphological differences between the other species possibly indicate either environmentally induced modifications (morphoclines) or gradual, anagenetic evolution.

Despite the poor preservation, *Adamussium jonkersi* sp. nov. easily can be differentiated from *A. auristriatum* by its weaker valve convexity, narrower umbonal angle, apparent asymmetry of auricles, and the fewer plicae, which are better-defined and more widely separated than in *A. auristriatum*, and with intercalated fine plicae observable only at the ventral margin of the valves. *Adamussium jonkersi* sp. nov. also differs from both subspecies *A. colbecki colbecki* and *A. colbecki cockburnensis* in its apparently procline valves, narrower umbonal angle, and the presence of radial costae on the RV anterior auricle.

Shell microsculpture. — The commarginal sculpture of *Adamussium jonkersi* sp. nov. is composed of distinct but weak lirae, in groups almost equally and closely spaced down the entire shell. Unlike other species of the genus, the microsculpture is not observed in SEM images (Fig. 6). Several explanations for this are possible, including the loss of ridgelets through ontogenetic development during life, the loss of this fragile microsculptural pattern during diagenetic recrystallization of the shell, or even because this microsculptural feature is absent (at least at the ventral margin of the available shell material studied under SEM).

Paleoecology. — According to Stanley (1970), pectinids with a swimming habit are characterized by an inequivalve condition, with the lower (right) valve being more convex than the upper valve, the presence of a thin shell with plicae, a broad umbonal angle (around 105° to 130°), and gapes adjacent to the auricles. Jonkers (2003), based on Stanley (1970), considered that swimming pectinids have an umbonal angle greater than 108° and a ratio between the anterior and posterior auricle lengths smaller than 1.7. However, Hayami (1991) stressed that the presence of radial folds results in an increase in drag coefficient. Stanley (1970) also affirmed that byssally attached pectinids, on the other hand, possess elongated anterior auricles, a byssal notch with no adjacent gapes, and a narrow umbonal angle. Of the features cited above, *A. jonkersi* sp. nov. displays an umbonal angle indicating that

specimens range from byssate to swimming habits (100° to 110°), an apparently slight inequivalve condition, and a rather thin shell with broad undulating plicae, which point to a free-swimming habit. The plicate shell, a character present in all *Adamussium* species other than *A. alanbeui*, increases frictional drag in the water, thus reducing swimming capability due to the high-energy demand for swimming (Hayami 1991). The auricles are apparently asymmetrical. However, because of the incomplete preservation of the fossils, the features that would point to a truly byssate habit, such as the presence of a ctenolium and a wide byssal notch adjacent to the anterior auricle, are not observable. Despite the poor preservation, we infer a free-living, non-active swimming habit for *A. jonkersi*. More specifically, we suppose that it had the ability to clap its valves in order to escape from a potential predator. However, this condition does not exclude the possibility that this scallop lived byssally attached during younger stages, as many pectinids do (Stanley 1970; Gould 1971).

Taphonomy. — The assemblage is composed of thin-shelled specimens, preserved as disarticulated, complete or partially fragmentary valves. The shells are in a convex-up orientation, concordant with bedding (Fig. 4). The sedimentological features of the unit indicates an estuarine environment to lower-energy tidal flat (Birkenmajer 1982). The disarticulation of the shells and their preservation in a convex-up orientation indicate lateral transport of the valves for a short distance due to traction currents. Indeed, as demonstrated by the experimental studies of McKittrick (1987) and Simões *et al.* (2006), convex shells always settle down in a concave-up (unstable) orientation. Hence, the convex-up attitude (stable orientation) of the shells in relation to bedding is achieved when waves, currents and bioturbation are present in the environment (Simões *et al.* 2006). Hence, despite their reclinant, free-living mode of life, the studied shells of *Adamussium jonkersi* are parautochthonous (*sensu* Kidwell *et al.* 1986), and were deposited in a low- to medium-energy environment.

Final comments

The modern representative of the genus *Adamussium*, *A. c. colbecki*, is an endemic Antarctic species with a circum-Antarctic distribution (Dell 1972, 1990), and is found in almost all sites protected from high-energy water conditions around Antarctica (Schiaparelli and Linse 2006). Some studies have shown that this Antarctic species is highly sensitive to temperature increase, suggesting that it is physiologically adapted to low environmental temperatures (Viarengo *et al.* 1999; Peck *et al.* 2004). Because its ancestral lineage can be traced back to the Oligocene, we conclude that this important component of the Recent Antarctic fauna probably had an evolutionary past related to the Cenozoic cooling history of the continent. In this way, the new taxon contributes to the knowledge of the fossil record of the genus and potentially will help future studies of environmental change in Antarctica during the Cenozoic.

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Nuculidae (Bivalvia) in the Cape Melville Formation, King George Island, Antarctica, with an overview of the bivalve fauna

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Abstract: Nuculid bivalves of the Cape Melville Formation (Early Miocene, King George Island) are reviewed. Ten bivalve taxa are listed from the formation in the families Nuculidae (two species), Sareptidae, Malletiidae, Limopsidae (two species), Limidae, Pectinidae, Hiatellidae, and Periplomatidae. The Nuculidae consist of two species of *Leionucula* Quenstedt, 1930. One of these, *L. melvilleana* n. sp., is described and the other consists of the two species named previously by Anelli *et al.* (2006), which are demonstrated to be synonymous and are assigned to the species *Leionucula frigida* (Anelli, Rocha-Campos, Santos, Perinotto & Quaglio 2006). This assemblage, dominated by protobranchs (89% of specimens), is a typical fauna of offshore soft substrates, with a few specimens transported from hard substrates nearby. The diversity of Nuculidae has decreased in the Antarctic region through the Cenozoic.

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Key words: biogeography, Cenozoic, Southern Ocean, taxonomy

Introduction

Antarctic Cenozoic fossil deposits give us important information about a period of environmental change in the Southern Hemisphere. This includes the final break-up of Gondwana, the onset of the Antarctic Circumpolar Current and the first major expansion of Antarctic ice (Zachos *et al.* 1992). Establishment of present-day oceanographic and atmospheric circulation patterns also took place in the Cenozoic (Ivany *et al.* 2008).

The Cape Melville Formation preserves one of the most important glacial faunal assemblages from Antarctica during the Cenozoic. Study of the British Antarctic Survey (BAS) Cape Melville Formation collection has increased our knowledge of the bivalve assemblage, which contributes to the overall community structure of the formation and of Antarctica in the Early Miocene. The exposures of the Cape Melville Formation on King George Island, located to the north-west of the Antarctic Peninsula (Fig. 1), preserve a Miocene marine invertebrate fauna. Few fossiliferous outcrops are found from this age in Antarctica (Beu 2009), therefore this assemblage is extremely important in understanding Cenozoic biodiversity in Antarctica. Along with the underlying Late Oligocene Destruction Bay Formation (Quaglio *et al.* 2010), the Cape Melville Formation provides a unique fossil record in the Antarctic Peninsula region during a latest Oligocene to earliest Miocene interglacial to glacial transition (Birkenmajer *et al.* 1983, Dingle & Lavelle 1998, Troedson & Riding 2002).

Geology and stratigraphy of the Cape Melville Formation

The Cape Melville Formation (Moby Dick Group, King George Island Supergroup) comprises a c. 150 m thick

exposure on the narrow Melville Peninsula, which lies at the eastern extremity of King George Island, West Antarctica (Troedson & Riding 2002) (Fig. 1). The unit consists of horizontal to sub-horizontally bedded mudstones and silty mudstones, which are characterized by a diverse assemblage of glacially rafted lithological material (Birkenmajer *et al.* 1983). It has been dated as 22.6 ± 0.4 Ma (Early Miocene) based on Sr isotope data from bivalves (Dingle & Lavelle 1998).

Overall, the assemblage has a deepwater, outer-shelf aspect (Förster *et al.* 1987, Feldmann & Crame 1998). The fauna includes gastropods (Karczewski 1987), solitary corals (Roniewicz & Morycowa 1985), a nephropid lobster (Feldmann & Crame 1998), crabs (Förster *et al.* 1987), brachiopods (Bitner & Crame 2002), bryozoans (Hara & Crame 2004), echinoids (Jesioneck-Szymańska 1987), scaphopods, polychaetes (Szaniawski & Wrona 1987) and bivalves (Jonkers 2003, Anelli *et al.* 2006, Whittle *et al.* 2011).

The Family Nuculidae

The Family Nuculidae Gray, 1824 belongs to the Protobranchia, a bivalve subclass that is an understudied but important component of extreme environments at the present-day. They are common in polar regions and the deep sea (Allen 1978). The family Nuculidae is also known from the shelf and slope, as well as abyssal depths (Allen 1978), and they are active infaunal deposit feeders (Rhind & Allen 1992). Nuculidae are characterized by small- to medium-sized, ovate to ovate-trigonal shells and taxodont dentition. The beaks are opisthogyrate, the ligament is internal and a resilifer is present. Ornamentation typically consists of fine radial striae, usually with a smooth, shiny periostracum in living forms

Fig. 1. a. Location of the South Shetland Islands, b. location of Cape Melville on King George Island, and c. Cape Melville geology and site localities (P. 2701, P. 2702 and P. 2707) for nuculid specimens from BAS and the Instituto de Geociências, Universidade de São Paulo (adapted after Feldmann & Crame 1998).

(Keen 1969). Nuculidae range in age from the Ordovician to the present (Keen 1969). There are many taxonomic issues within this family based on the low numbers of polymorphic shell characters (McAlester 1964, Rhind & Allen 1992, Beu 2006). To date there have been no molecular phylogenetic or barcoding analyses (Beu 2006), so morphological aspects are currently used to identify modern genera and species. A problem with studying the morphology of the Nuculidae is that they retained primitive characters as they are well adapted to their environment (McAlester 1964) and this conservatism in evolution, at the species and the genus level, means that they are difficult to characterize for taxonomic and phylogenetic analysis (McAlester 1964, Rhind & Allen 1992, Beu 2006). Nuculids from King George Island have been described from the Cape Melville Formation by Anelli *et al.* (2006). The material was placed into two species of the genus *Ennucula* Iredale, 1931, but was subsequently re-assigned by Beu (2009) to the genus *Leionucula*.

In this paper the composition of an assemblage of Cape Melville fossil bivalves from the BAS collections is identified and a new species is described.

Methods

Cape Melville Formation bivalve specimens were collected by J. Alistair Crame in the 1994–95 field season. Bivalve specimens are housed in the BAS collections, Cambridge, under the prefixes P. 2701 (22 specimens), P. 2702 (751 specimens) and P. 2707 (123 specimens), the locations for which are shown in Fig. 1.

Bivalves in the BAS assemblage were studied using an optical microscope, measured using Vernier callipers, drawn with the aid of a camera lucida and photographed using a digital camera. The BAS bivalve specimens were also compared to those held at IGc-USP (Instituto de Geociências, Universidade de São Paulo), especially with

Fig. 2. Distribution of Nuculidae in the southern high latitudes. **a.** Nuculid records at the present-day. **b.** Nuculid records through time. Colours represent genera, shapes represent time periods.

the type material. These are housed in the Coleção Científica (Scientific Collection) of the Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências,

Universidade de São Paulo, under the prefix GP/IT and GP/IE (Anelli *et al.* 2006).

Length of the shell was measured by taking the greatest distance along the antero-posterior axis. Height was the greatest measurement at right angles to the length and inflation was measured by taking the maximum measurement of two valves together in complete specimens. A total of 542 nuculid specimens from three locations in the Cape Melville Formation were studied. All available specimens per locality were measured, unless they had undergone significant distortion or flattening. SCAR-MarBIN (www.scarmarbin.be, accessed February 2011) was used to access data on the distribution of recent nuculids in Antarctica and the southern high latitudes (Bouchet 2012). SOMBASE-GSCM (the Cenozoic Marine Fauna Database, developed by H. Griffiths, BAS) and the Paleobiology Database (<http://paleodb.org/cgi-bin/bridge.pl>, accessed February 2011) were used to access data on the distribution of fossil nuculids. These occurrences were checked against the original published literature (Ihering 1897, Ihering 1907, Wilckens 1910, Doumani *et al.* 1965, Dell & Fleming 1975, Gaździcka & Pugaczewska 1984, Zinsmeister 1984, Stilwell & Zinsmeister 1987, 1992, Pickard *et al.* 1988, Zinsmeister & Macellari 1988, Beu & Maxwell 1990, Del Río & Camacho 1996, Del Río & Chiappara 1998, Taviani *et al.* 2000, Stilwell 2000, 2003, Taviani & Beu 2001, Stilwell *et al.* 2004, Anelli *et al.* 2006, Beu 2009).

Southern high latitude Nuculidae

The four genera belonging to the Family Nuculidae that are currently found in southern high latitude waters (Fig. 2a) are *Austronucula* Powell, 1939, *Ennucula*, *Nucula* Lamarck, 1799 and *Pronucula* Hedley, 1902. The nuculids have a high

Fig. 3. Time ranges of southern high latitude nuculid genera (grey), with Antarctic genera (black), through the Cenozoic.

Table 1. The BAS Cape Melville Formation bivalve fossils.

Order	Family	Genus	Species	Reference	BAS specimens
Nuculoida	Nuculidae	<i>Leionucula</i>	<i>frigida</i>	Anelli <i>et al.</i> 2006	495
		<i>Leionucula</i>	<i>melvilleana</i>	This paper	41
		Indeterminate	Indeterminate		6
Nuculanoida	Sareptidae	<i>Yoldia</i>	<i>peninsularis</i>	Anelli <i>et al.</i> 2006	148
	Mallettiidae	<i>Neilo (Neilo)</i>	<i>rongelii</i>	Anelli <i>et al.</i> 2006	69
	Indeterminate	Indeterminate	Indeterminate		39
Arcoida	Limopsidae	<i>Limopsis</i>	<i>psimolis</i>	Anelli <i>et al.</i> 2006	3
		<i>Limopsis</i>	<i>infericola</i>	Whittle <i>et al.</i> 2011	4
		<i>Limopsis</i>	Indeterminate		4
Pectinoida	Pectinidae	<i>Adamussium</i>	<i>alanbeui</i>	Jonkers 2003	1
Limoida	Limidae	<i>Limatula</i>	sp.		1
		(<i>Antarctolima</i>)			
Myoida	Hiatellidae	<i>Panopea</i>	sp.		17
		? <i>Panopea</i>	Indeterminate		14
Pholadomyoida	Periplomatidae	<i>Periploma</i>	<i>acuta</i>	Anelli <i>et al.</i> 2006	9
Indeterminate	Indeterminate	Indeterminate	Indeterminate		45
					Total 896

species-richness north of the Antarctic Polar Front and a lower species-richness south of the Polar Front (dominantly of the genus *Nucula*, but occurrences of *Pronucula* and *Ennucula* have also been found near the South Shetland Islands) (Fig. 2a) (Linse *et al.* 2006, Bouchet 2012). Specimens are mostly identified from the Antarctic Peninsula region and occur in water depths of 6–4209 m (Dell 1990). At present Nuculidae are species rich in waters around New Zealand and South America (Bouchet 2012).

The oldest recorded occurrence of a fossil nuculid in the southern high latitudes is of *Nuculoidea* Williams & Breger, 1916, which is Lower Devonian in age; it was collected from the Ohio Range in Antarctica (Doumani *et al.* 1965) (Fig. 2b). Apart from a Jurassic record of *Nucula* from the Antarctic Peninsula, the rest of the fossil Antarctic nuculids are from the Cretaceous period and younger, and most are Cenozoic (Figs 2b & 3). Ten genera of fossil nuculids have been found in the southern high latitudes in the Cenozoic, with six of these genera occurring in rocks from Antarctica (Figs 2b & 3). However, New Zealand fossil nuculid diversity is significantly greater than the published diversity (A. Beu, personal communication 2012). Generic diversity has decreased in the southern high latitudes through time as only three genera occur south of the Polar Front at the present-day (Fig. 2a).

Antarctic fossil species (Figs 2b & 3) have been found from the drill cores DSDP 270 (Dell & Fleming 1975) and CRP-2/2A (Taviani *et al.* 2000), plus in the vicinity of Mount Discovery (Stilwell 2000), which are all in the McMurdo Sound region and also from the Antarctic Peninsula region (Wilckens 1910, Stilwell & Zinsmeister 1987, Zinsmeister & Macellari 1988, Stilwell & Zinsmeister 1992, Stilwell *et al.* 2004, Anelli *et al.* 2006), Marine Plain (Pickard *et al.* 1988) and the Ohio Range (Doumani *et al.* 1965).

Nuculids occurred sporadically through the Cenozoic in the southern high latitudes (Fig. 3) in units deposited in a

variety of water depths. No genus has a continuous fossil record through the Cenozoic to the present. The fossil record in Antarctica is very patchy, with most occurrences in the Eocene–Miocene periods (Fig. 3). There are no Antarctic fossil occurrences in the Pleistocene or Holocene, probably related to glaciation in Antarctica. Generic diversity of the family Nuculidae decreased in the Antarctic region through the Cenozoic to the Recent (Fig. 2). The cause of this decrease in diversity is unknown but it may have been related to environmental reasons such as changes in oceanic circulation or extension of ice sheets onto continental shelves, which led to a change in species composition.

The BAS Cape Melville Formation bivalve assemblage

The BAS Cape Melville Formation bivalve assemblage consists of 896 specimens. Of these 770 specimens have been identified to species level, 783 to genus, 851 to family and 45 fossil specimens were too badly preserved to be assigned (Table 1). In total eight bivalve families have now been identified from the Cape Melville Formation: Nuculidae, Sareptidae, Mallettiidae, Limopsidae, Pectinidae, Limidae, Hiattellidae and Periplomatidae. Generally families in the Cape Melville Formation bivalve assemblage are monospecific, except for the Limopsidae and Nuculidae, which are both represented by two species (Table 1).

Overall, ten species of bivalve have been identified from the BAS Cape Melville collection (Table 1). Of these, one species was originally identified by Jonkers (2003) and seven species by Anelli *et al.* (2006). Five of the species originally identified by Anelli *et al.* (2006) are also in BAS collection, and two species of nuculid are re-assigned and synonymized into the species *Leionucula frigida* (Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, 2006) (see Systematics below), based on new data from the BAS nuculid collection. A second taxon of nuculids can be identified from the BAS Cape

Fig. 4. Shells of *Leionucula frigida* from the BAS collection. a.–c. P. 2702.340, a. left valve, b. posterior, c. anterior. d.–f. P. 2702.341, d. left valve, e. posterior, f. anterior. g. P. 2702.339 left valve. Scale bar = 2 mm.

Melville Formation assemblage, specimens are described as *Leionucula melvilleana* n. sp. (see Systematics below).

Following study of the BAS collection a further two species are recorded from the unit, *Limopsis infericola* Whittle, Linse & Griffiths, 2011, and *Limatula* (*Antarctolima*) sp. *Leionucula frigida* is the most abundant species, with 495 specimens, *Yoldia peninsularis* is the second most abundant with 148 specimens. The Limidae and Pectinidae are represented by only one specimen each (Table I). Overall protobranch bivalves dominate the Cape Melville Formation bivalve

assemblage as they comprise 89% of the BAS collection. As a family, the Nuculidae constitute 60% of the collection.

Systematics

Class Bivalvia Linnaeus, 1785
 Order Nuculida Dall, 1889
 Family Nuculidae Gray, 1824
 Subfamily Nuculominae Maxwell, 1988
 Genus *Leionucula* Quenstedt, 1930

Fig. 5. Shell morphometrics of Cape Melville Formation Nuculidae.

Anelli *et al.* (2006) described two species of nuculid under the names *Ennucula frigida* and *E. musculosa*, based on 84 well preserved specimens. However, several authors have suggested *Ennucula* and *Leionucula* are synonymous (e.g. Keen 1969, Stilwell 2000, Beu 2009). Based on this, Beu (2009) stated that the Cape Melville species of Nuculidae, *E. musculosa* and *E. frigida*, should be re-assigned to the genus *Leionucula*.

Type species: (by original designation) *Nucula albensis* d'Orbigny

Leionucula frigida (Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, 2006)
(Fig. 4)

2006 *Ennucula frigida* Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, pp. 117–119; Fig. 5.

2006 *Ennucula musculosa* Anelli, Rocha-Campos, Santos, Perinotto & Quaglio, pp. 119–120; Fig. 6.

Diagnosis of species: Umbones slightly elevated above hinge line with opisthogyrate beaks, external ornament of fine growth lines overlain by well-marked irregularly spaced commarginal growth corrugations; with a maximum of 20 teeth in the anterior and ten on the posterior regions of the shell; chondrophore short and oblique.

Material examined: 495 specimens from the BAS Cape Melville Formation collection and 15 specimens originally described as *E. frigida* and *E. musculosa* in Anelli *et al.* 2006 from the Instituto de Geociências, Universidade de São Paulo.

Localities: BAS localities P. 2701, P. 2702 and P. 2707, plus section C and D of Anelli *et al.* 2006 (Fig. 1).

Discussion: The BAS collection includes 495 specimens with morphological similarity to the previously described species *E. musculosa* and *E. frigida* (Figs 4 & 5). One of the criteria for the separation of these two species was specimen size, as the IGC-USP specimens fit into two discrete size categories (see *E. frigida* and *E. musculosa* datasets on Fig. 5) (Anelli *et al.* 2006). However, further evidence from the large BAS collection of nuculids has increased our knowledge of the shell morphology and size ranges for Cape Melville nuculids. The BAS specimens of *L. frigida* show a much wider range in shell size than specimens originally described as *E. frigida* and *E. musculosa* (Anelli *et al.* 2006) and there is no distinct division in the BAS data (Fig. 5). Other criteria used to separate the two species were slight differences in margin shape and angles (Anelli *et al.* 2006). However, as with shell size, BAS specimens also show a range in margin morphology that incorporates the *E. frigida* and *E. musculosa* end members of Anelli *et al.* (2006). Therefore, it is not possible to separate the BAS specimens into two species using the descriptions in Anelli *et al.* 2006. Simple morphometric comparisons demonstrate that *E. musculosa* intergrades with *E. frigida*, and we regard the species names *musculosa* and *frigida* as synonymous. As first revisers, we choose the name *Leionucula frigida* for this species.

Leionucula melvilleana n. sp.
Whittle & Quaglio, 2012
(Fig. 6)

Derivation of name: Named for the Melville Peninsula, where the specimens were discovered.

Fig. 6. *Leonucula melvilleana* n. sp. a.–c. Holotype, P. 2702.1321, a. left valve, b. posterior, c. anterior. d.–f. Paratype P. 2702.1322, d. left valve, e. posterior, f. anterior. g. P. 2702.1323 left valve. h. Internal mould P. 2702.1328. Scale bar = 2 mm.

Diagnosis: Large inflated nuculid, with a straight posterior margin.

Holotype: P. 2702.1321 complete articulated shell.

Paratypes: P. 2702.1322, P. 2702.1323, P. 2702.1324, internal mould P. 2702.1328, and partial specimen P. 2702.1329, which was cut in two to see the taxodont dentition. Type specimens are housed in the BAS Type and Figured collection.

Other material: P. 2702.1325–1327; P. 2702.1330–1334 and P. 2702.1097–1113, P. 2702.1115–1117, P. 2702.

1119–1122; P. 2702.1148, P. 2702.1149, which are housed at BAS, and specimen GP/IE 5252, from the Instituto de Geociências, Universidade de São Paulo.

Locality: King George Island, South Shetland Islands, Antarctica. Cape Melville Formation, Moby Dick Group 62°02'S, 57°38'W, locality P. 2702 and section C of Anelli *et al.* 2006 (Fig. 1).

Age: 22.6 ± 0.4 Ma (Early Miocene) based on Sr isotope data from bivalves (Dingle & Lavelle 1998).

Description: Shell longer than high, antero-posteriorly elongate. Length 25–39.5 mm (mean 30.5 mm, SD = 4.7;

holotype length 37.4 mm), height 21–36 mm (mean 25.0 mm, SD = 4.1; holotype height 28 mm), inflation 13.5–23.1 mm (mean 17.4 mm, SD = 2.8; holotype inflation 23.1 mm) (Fig. 5). Umbones somewhat elevated above the hinge line, with slightly curved opisthogyrate beak. Posterior margin almost straight, anterior margin curved, ventral margin broadly rounded. Posterior adductor rounded; anterior adductor sub-quadrate, larger than posterior, with a very clear margin (Fig. 6h). Non-sinuate pallial line. External sculpture of irregularly spaced coarse commarginal growth lines, inner ventral margin smooth. Taxodont dentition visible on some specimens, posterior part of hinge short, with at least seven teeth (GP/IE 5252), anterior part hinge, with at least 15 (P. 2702.1325) to 19 teeth (GP/IE 5252).

Remarks: Specimens are similar to a single *Leionucula* specimen from Eocene erratics of McMurdo Sound identified by Stilwell (2000), who suggested that it may belong to a new species but did not formally describe it. The McMurdo specimen falls within the length, height and inflation range of the Cape Melville specimens. However, *L. melvilleana* n. sp. differs in having a straighter posterior margin. *Nucula* (*Leionucula*) *grandis* Malumian, Camacho & Gorroño, 1978 is also similar in size to *L. melvilleana* n. sp., but differs in having a subrectangular as opposed to subtriangular outline and more pointed umbones (Malumian *et al.* 1978).

The new species differs from specimens belonging to the nuculid genera *Nucula* Lamarck, 1799, *Lamellinucula* Schenck, 1944, *Linucula* Marwick, 1931, *Deminucula* Iredale, 1931, *Pronucula* Hedley, 1902, *Pectinucula* Quenstedt, 1930, *Gibbonucula* Eames, 1951 and *Rumptonucula* Bergmans, 1978 as it has a smooth as opposed to crenulate inner ventral margin (Rhind & Allen 1992). *Acila* (Adams & Adams, 1858) differs from the new species as it has divaricate sculpture (Rhind & Allen 1992).

Leionucula melvilleana n. sp. differs from the *L. frigida* previously described from the Cape Melville Formation by its greater height and length (Fig. 5). *Leionucula melvilleana* specimens are generally more inflated than *L. frigida*, but there is some overlap. Measurements of *L. melvilleana* and *L. frigida* were analysed using unpaired *t*-tests. The two species show highly significant differences for height, length and inflation (length $P = 9.04 \times 10^{-14}$, height $P = 8.80 \times 10^{-13}$, inflation $P = 1.18 \times 10^{-47}$). The *L. melvilleana* specimens have less pronounced commarginal ridges than *L. frigida*. They also have a straighter beak, antero-dorsal margin, and posterior margin. Also, the muscle scars are a different shape and the anterior adductor is much less rounded on *L. melvilleana* n. sp.

Conclusions

The Cape Melville Formation, one of the earliest Cenozoic glacial faunas from Antarctica, preserves a bivalve assemblage that was dominated by protobranchs. The Family Nuculidae, represented by two species, is the most numerous in the unit,

with most specimens belonging to *L. frigida*. The fauna of the Cape Melville Formation has been extended by the addition of *L. melvilleana* n. sp. These results increase our knowledge of the Cape Melville Formation fossil assemblage, as well as contributing to knowledge of the overall Antarctic fossil community. Analysis of the Cenozoic fossil record indicates that the generic diversity of the Family Nuculidae has decreased in the Antarctic region through the Cenozoic to the Recent.

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Anexo 6

FERNANDA QUAGLIO, LUIZ E. ANELLI, SILVIO NIHEI, ROWAN J. WHITTLE, HUW GRIFFITHS, KATRIN LINSE, MARCELLO G. SIMÕES & ANDRZEJ GAŹDZICKI. Bivalves from the Cape Melville Formation (early Miocene, West Antarctica): new taxa and paleobiogeography. *Em preparação.*

BIVALVES FROM THE CAPE MELVILLE FORMATION (EARLY MIOCENE, WEST ANTARCTICA): NEW TAXA AND PALEOBIOGEOGRAPHY

Abstract

The fossiliferous Cape Melville Formation preserves an important record of the Cenozoic glacial history of Antarctica. Molluscs are the most diverse and abundant group in the unit. Nine bivalve genera were so far recorded in the unit. In this paper we describe three new bivalve taxa from the Cape Melville Formation and analyze the paleobiogeographic distribution of the identified genera along the Cenozoic in the high latitudes of Southern Hemisphere. We found that the shelfal bivalves from the Cape Melville Formation were extinct from Antarctic waters after early Miocene or early Pliocene. This disagrees of previous scenarios of extinctions occurring along the Cenozoic, related to the long-term Cenozoic glacial history of Antarctica. The extinctions would have occurred after the expansion of ice shelves in Antarctica, during the Plio-Pleistocene glaciation event. Those Cape Melville genera currently living in Antarctic comprise euribathic representatives that were not affected by the ice-shelf advance during Neogene, with several present-day species thriving also in Antarctic periphery.

Keywords: Cape Melville Formation, early Miocene, bivalves, *Offadesma*, paleobiogeography, Antarctica.

Introduction

The South Shetland Islands, mainly the King George Island (**Fig.1**), preserve some key records of the Cenozoic glacial events related to the onset of West Antarctic Ice Sheet. The Cape Melville Formation provides the single western geological record of the earliest Miocene glaciation episode in Antarctica (Birkenmajer *et al.* 1983, Birkenmajer 1985, Dingle and Lavelle 1998), which is coupled with a global cooling supported by oxygen-isotope data (event Mi-1 of Miller *et al.* 1991). Hence, together with other Cenozoic invertebrate fauna described in Antarctica and peripheral regions, the Cape Melville fossil record can be used in order to investigate how marine faunas responded to climatic changes of the last global switch from greenhouse to icehouse conditions.

Many fossils were already recorded in the Cape Melville Formation (see next section, Table 1), being the molluscs the most diverse and abundant group (Karczewski 1987, Anelli *et al.* 2006, Whittle *et al.* 2011, 2012). Although the bivalves were previously described, new discoveries presented herein show that the group is more diverse in the Cape Melville Formation than formerly thought. The new findings enhance our knowledge of Antarctic mollusc diversity during the Miocene, a time-interval with rare fossiliferous deposits in Antarctica.

Previous ideas suggest that a shallow marine paleobiogeographic province - the “Weddellian Province” - would have existed in the southernmost region from the Cretaceous to the Eocene encompassing the southern Australia, Antarctica, New Zealand and southern South America (Zinsmeister 1979). The marine fauna of the Cape Melville Formation would have witnessed a scenario of post Weddellian province break-up, in which extensive glaciations caused near-shore taxa to extinct along the Cenozoic and to be restricted to Subantarctic areas until the present day (Beu 2009).

In this paper we describe three new bivalve taxa from the Cape Melville Formation and analyze the fossil record of the identified genera along the Cenozoic in the southern oceans. The main aims are to contribute to the knowledge of the Antarctic Cenozoic bivalves and to access their paleobiogeographic evolution during critical time intervals of environmental changes tied to the geographic isolation and cooling of Antarctica.

FIGURE 1 HERE

The Cape Melville Formation

The Cape Melville Formation is the youngest unit of the Moby Dick Group (Birkenmajer 1982, 1984) and comprises a 150m thick succession cropping out along the Melville Peninsula, at east side of King George Island, West Antarctica (**Fig. 1**). The unit is interpreted as a glaciomarine succession that records a maximum glacial event at the base followed by a glacial retreat with distal glaciomarine facies at the top (Birkenmajer 1982, 1984, Troedson and Riding 2002).

Dating based on foraminifer content indicated early Miocene for the upper part of the unit (Birkenmajer and Łuczkowska 1987), an age corroborated by Sr-isotopic dating based on bivalve shells (22.6 Ma, Dingle and Lavelle 1998).

According to the description by Troedson and Riding (2002), the Cape Melville Formation comprises four units (A to D) from base to top. The base ("unit A") reaches around 25m thick and is marked by diamictites intercalated with sandstone facies containing foraminifera and diatom fragments. Unit A is interpreted as glaciogenic debris flows in proximal glaciomarine conditions during a maximum glacial event. The next 30m of the succession, named "unit B", are composed by thinner beds of diamictites and muddy sandstones, as well as mudstone beds, with rare or absent exotic clasts. This unit records marine invertebrates (bivalves and corals according to Birkenmajer 1984) and ichnofossils. Fossil beds were generated in the context of proximal glaciomarine conditions, but during a glacial retreat. The following 30m ("unit C") are made up by silty sandstones to sandy siltstones with common exotic clasts recording several marine invertebrates (bivalves and gastropods according to Birkenmajer 1984). This unit is interpreted as deposited by gravity-driven flows, turbidity currents and air-fall debris originated from eruptive events.

The top of the succession is around 50m thick ("unit D") and is marked by the presence of siltstones interbedded with thin shales and fine sandstones, recording abundant crustaceans, gastropods, bivalves, corals, diatoms and dinoflagellate cysts (and, according to Birkenmajer 1984, also fish remains, ichnofossils and reworked Cretaceous belemnites). Both units C and D are interpreted as deposited during a glacial retreat, but in a distal marine, hemipelagic environment.

The succession was intensely affected by faulting (Birkenmajer 1994). Even though some of the fossil sites were partially correlated, difficulty of access and the presence of ice-covered areas mar the secure stratigraphic correlation of all localities (see Birkenmajer 1984, fig. 7, p. 19).

Tables 1 and 2 and Figure 1B-C summarize the invertebrate macrofossils in each of the several fossiliferous localities of the Cape Melville Formation, according to data collected by the authors and from literature. The bivalve material described herein is mostly preserved in low to high number, sparsely in the basal portions or more abundantly as clusters in the upper part of the unit (Birkenmajer 1984, Troedson and Riding 2002, Anelli et al. 2006).

TABLE 1 HERE

Bivalve fossil record

Nine genera in eight bivalve families were so far identified in the CMF (Tables 1 and 2; Fig. 1B-C). Jonkers (2003) described the pectinid *Adamussium alanbeui* that was recently reassigned to *Antarctipecten alanbeui* by Beu and Taviani (2013). Anelli *et al.* (2006) described the nukulids *Ennucula frigida* and *Ennucula musculosa*; the malletid *Neilo (Neilo) rongelii*; the sareptid *Yoldia peninsularis*; the limopsid *Limopsis psimolis*; the hiatellid *Panopea (Panopea) sp. cf. P. regularis*; and the periplomatid *Periploma acuta*. Whittle *et al.* (2011) erected the limopsid *Limopsis infericola* and synonymized one specimen to *L. infericola* previously attributed to *Limopsis psimolis* by Anelli *et al.* (2006). Whittle *et al.* (2012) erected the nukulid *Leionucula melvilleana*.

TABLE 2 HERE

Material and Methods

Bivalve specimens studied in the systematic session were collected from the erosional top of the Melville Peninsula by A. Gaździcki, K. Rolnicki and R. Wrona during the 5th Polish Antarctic Expedition to Arctowski Station in the austral summer of 1980-81, and by J. Alistair Crame, in the 1994-95 BAS expedition. Thirty one specimens, mainly internal moulds, are housed in the collections of the Institute of Paleobiology (PAS) in Warszawa, Poland, under catalogue number ZPAL/L12/A, B and E. One specimen, an internal mould with partially preserved shell material, is housed in the British Antarctic Survey (BAS) in Cambridge, United Kingdom, under number P.2702.779.

Specimens were measured with reference to the hinge line: the length, height and width are in relation to the greatest measured lines parallel, perpendicular and orthogonal to the hinge line, respectively. Size, elongation and obesity indexes were calculated according to Stanley (1970). Systematic classification according to Bieler *et al.* (2010).

For the paleobiogeographic analysis we gathered information on bivalve genera recorded in the Cape Melville Formation (from Anelli *et al.* 2006, Whittle *et al.* 2011, 2012, Beu and Taviani 2013, and this work; see Fig. 1 and Table 2). Occurrences of Melville genera in other geological units from Cretaceous to Pleistocene were collected from SOMBASE-GSCM (the Cenozoic Marine Fauna Database, Griffiths *et al.* 2003), the Paleobiology Database (<http://paleodb.org>) and from additional references lacking in

both databases (eg. Griffin and Pastorino 2006, Aguirre *et al.* 2008, Quaglio *et al.* 2008, 2010, Whittle *et al.* 2011, 2012, Beu 2009, Beu and Raine 2009, Beu and Taviani 2013). Data on extant genera were obtained from SCAR Mar-BIN (<http://www.scarmarbin.be/>) and Spencer *et al.* (2011). Only southern marine areas were considered: Southern South America, Antarctica (East and West), New Zealand and Australia. West Antarctica includes outcrops found in Antarctic Peninsula (King George, Seymour, James Ross and Vega islands) and East Antarctica includes McMurdo drill holes and McMurdo Erratics in McMurdo Sound, and Marine Plain in Vestfold Hills.

The cluster analysis was performed using non-transformed presence only data with quantitative Bray-Curtis Similarity (Bray and Curtis 1957) with PRIMER v6 (Clarke and Gorley 2006), analyzing genera similarity according to their occurrences through space (localities) and time (time periods from Cretaceous to Recent).

The distributional patterns were spatially represented using panbiogeographic tracks (Craw *et al.* 1999). The individual tracks (one track per genus) were drawn with plotted data from latitudes presently higher than 34°S in paleogeographical reconstructions by Winterton & Livermore (2004) from late Cretaceous to Recent, therefore allowing viewing the dynamic distributional changes through the entire time-interval.

Paleontology

Background of the New Taxa

Limopsidae

Limopsidae comprises a cosmopolitan family (Newell 1969) at present-day oceans, being most of the representatives abyssal and cold-water species of the genus *Limopsis* (Morton 2013). The oldest limopsid record is assigned to middle Jurassic of England and Europe (Tevesz 1977). Although the origin of Limopsidae was traced to Grammatodontidae (Tevesz 1977), no molecular phylogeny of the family is currently available (Morton 2013), and the taxonomic position of the family is contentious. Traditionally it is included in the Superfamily Limopsoidea of the Order Arcoida with Limopsidae, Glycymerididae, Manzanellidae and Philobryidae (Newell 1969) or with Philobryidae and Pichleridae (Amler 1999). More recently only Limopsidae and

Philobryidae form the Limopsoidea, a superfamily which no longer belongs to the Order Arcoida, but to Arcida (Bieler et al. 2010).

The family has a prolific Cenozoic record in the southern oceans. In New Zealand it is represented by 19 species in the genera *Limopsis*, *Notolimopsis* and *Pectunculina*, from the Cretaceous to Recent (Beu and Raine 2009). In Antarctica, South America and Australia, the family is represented solely by the genus *Limopsis*. Recently, Whittle et al. (2011) revised the fossil record of *Limopsis* focusing in the southern oceans and recognized 38 fossil species distributed in Antarctica, New Zealand, Australia and South America from Cretaceous to Pleistocene. In Antarctica, the genus is recorded from late Cretaceous, middle Eocene, early Oligocene, early Miocene, early Pliocene and Pleistocene deposits. In Australia, the genus occurs in late Paleocene, middle to late Eocene, early and middle Miocene, Pliocene and Pleistocene. In South America, it occurs in late Oligocene and late Miocene deposits of Argentina. Based on fossil and data on extant limopsids, Whittle et al. (2011) suggested that the Present-day southern distribution of the family is resulted from origination or migration and diversification of the group in the Southern Ocean.

Limidae

The Family Limidae is a monophyletic group (Giribet and Wheeler 2002) consisting of the single family of the Superfamily Limoidea in the Order Limida (sensu Bieler et al. 2010; equivalent to Limoida sensu Amler 1999). It comprises cosmopolitan shallow to deep water forms (Cox and Hertlein 1969, Dell 1990), with the oldest fossil record assigned with doubt to *Palaeolima* sp. from Devonian of Germany (Amler et al. 1990).

Southern records of the family include Carboniferous to Pleistocene and Recent from South America; late Permian, Triassic, Cretaceous and Paleocene to Recent of Australia; Permian to Pliocene and Recent of New Zealand; and Cretaceous, Paleocene, Eocene, Oligocene and Recent of Antarctica (The Paleobiology Database, www.paleodb.org; Atlas of Living Australia, <http://www.ala.org.au>; Spencer et al. 2011; Gofas 2012a).

In Australia, Cenozoic fossil genera include *Limea*, *Limatula* and *Lima* from Paleocene, Miocene and Pleistocene deposits (Buonaiuto 1977, Darragh 1977, Ludbrook 1953, 1983), all of them occurring in early Miocene deposits (Tate 1886).

New Zealand limids include eight Cenozoic fossil genera (*Acesta*, *Ctenoides*, *Divarilima*, *Lima*, *Limaria*, *Limatula*, *Limea* and *Notolimea*), with *Acesta*, *Lima* and *Limatula* occurring in early Miocene (Beu and Maxwell 1990).

Data on Cenozoic limids from southern South America include *Pseudolimea* from early Paleocene of Chubut (Kiessling et al. 2005), *Acesta* from early Eocene of Patagonia (Griffin 1991), *Limaria* and *Limatula* recorded from the late Oligocene to the early Miocene deposits of Patagonia (Del Río 2004), and *Limatula pygmaea* from Holocene at southernmost Tierra del Fuego (Gordillo et al. 2005), a species that presently lives in Magellan waters (Page and Linse 2002).

In Antarctica limid fossils include *Acesta webbi* and *Seymouritula antarctica* from the Cretaceous to Paleocene López de Bertodano and Sobral formations in Seymour Island (Zinsmeister and Macellari 1988), *Acesta bibbyi* and *Acesta (Antarcticesta) laticostata* from the Eocene La Meseta Formation at Seymour Island (Stilwell and Zinsmeister 1992, Beu 2009), and *Limatula (Antarctolima) sp.* and *L. (Antarctolima) ferraziana* from the early Oligocene Polonez Cove Formation at, respectively, Lions Rump and Vauréal Peak localities of the King George Island (Quaglio et al. 2008, Beu 2009).

Periplomatidae

The Family Periplomatidae is considered a monophyletic group with the Laternulidae as its sister-group, both constituting with the Thraciidae the Superfamily Thracioidea (Harper et al. 2000). The fossil record goes back to the Upper Cretaceous and modern representatives are cosmopolitan (Cox et al. 1969).

In New Zealand, Australia and Tasmania the Family Periplomatidae is recorded under *Periploma (Offadesma) marwicki* from the middle Eocene, *Periploma (Offadesma) angasi* from the early Oligocene to Recent (Morton 1981, Beu and Maxwell 1990) and *Periploma machphersoni* Marwick, 1931 in middle to late Miocene (Marwick 1931). *Periploma (Offadesma) angasi* Crosse and Fischer, 1864 is an uncommon infaunal suspension-feeder living in shoreface areas of New Zealand and Australia (Morton 1981). New Zealand and Australia also records the living *Pendaloma micans* Hedley, 1901, a periplomatid with a small and ovoid shell (Marshall 2002).

In South America, Periplomatidae fossils include *Anatina suborbicularis* from Tertiary deposits in Millanejo and *A. davilae* and *A. araucana* in Lebu, Central Chile

(Philippi 1887). According to Griffin (1991), those three species belong to the subgenus *Periploma* (Aelga) Slodkevich, 1935. However, Griffin and Pastorino (2006) held that *Anatina suborbicularis* may be possibly referable to *Offadesma*. The species *Periploma* (Aelga) *primaverensis* Griffin, 1991 occur rarely in the Eocene Río Turbio Formation of southern South America (Griffin 1991). *Offadesma* sp. was recorded from the late Oligocene-early Miocene Monte León Formation at southern Patagonia, Argentina and *Offadesma isolatum* Griffin and Pastorino, 2006 was recorded from the late Miocene Puerto Madryn Formation at northern Patagonia, Argentina (Griffin and Pastorino 2006). The Recent *Periploma compressa* Orbigny, 1846 and *P. ovata* Orbigny, 1846 occur in both Argentina and Brazil (Rios 1994).

Fossil record in Antarctica includes *Periploma* sp. that occurs in the Paleocene Sobral Formation at Seymour Island (Stilwell 2003, Stilwell *et al.* 2004), *P. topei* from the Eocene La Meseta Formation at Seymour Island (Zinsmeister 1984, Stilwell and Zinsmeister 1992), *Periploma* cf. *P. topei* from Eocene McMurdo Erratics (Stilwell 2000), *Periploma* sp. from the early Oligocene CRP-2/2A and CRP-3 (Taviani *et al.* 2000, Taviani and Beu 2001), *Periploma* (*Pandaloma*?) sp. from the Oligocene DSDP LEG 28, site 270 (Dell and Fleming 1975) and *P.* from the early Miocene Cape Melville Formation (Anelli *et al.* 2006). However, the identification of the Eocene Periplomatidae specimens is doubtful due to the absence of internal features and the quadrate shape which suggests greater affinity to Thraciidae than to Periplomatidae, as previously pointed out by other authors (Taviani *et al.* 2000, Griffin and Pastorino 2006). No Recent periplomatid is recorded in Antarctica; the closest relative is the thraciid *Thracia meridionalis*, with circum-antarctic distribution (Bouchet and Huber 2013).

Systematic Paleontology by Quaglio, Anelli and Whittle

Class Bivalvia Linnaeus, 1758

Subclass AUTOBRANCHIA Grobben, 1894

Superorder PTERIOMORPHIA Beurlen, 1944

Order ARCIDA Gray, 1854

Superfamily LIMOPSOIDEA Dall, 1895

Family LIMOPSIDAE Dall, 1895

Genus *Limopsis* Sassi, 1827

Type-species. *Arca aurita* Brocchi, 1814

Limopsis sp.

Figure 2, Table 3

Material. Two internal molds of conjugated valves and one internal mold of right valve (ZPAL L/12/A/30, L12/C/15, L12/G/9).

Locality. PG below Grzyb: L12/G/9, A-322: L/12/A/30, East IV: L12/C/15 (localities J, K and L of **Fig. 1** and **Table 2**), Cape Melville Formation, Melville Peninsula, King George Island, West Antarctica.

Age. Early Miocene.

Description. Internal mould small, with thick shell remains, subcircular, slightly oblique anteriorly, slightly inequilateral; moderately elongate (mean 1.10), compressed (mean 1.82). Umbones inconspicuous, with anterior and posterior carinas forming an angle of around 100°; beaks orthogyrous. Dorsal margin long, posterior dorsal margin longer than anterior; ventral margin rounded. External ornamentation of 1-2mm width radial costae. Inner surface striated as seen in internal moulds; inner ventral margin with very faint crenulations (as seen in specimens L12/A/30 and L12/G/9). Two well-defined depressions, interpreted as myophoric ridges, run radially close to anterior and posterior dorsal margins, creating elongate areas where the adductors are attached. Anterior adductor of medium size, well marked, elongate; posterior adductor broad, faintly marked, elongated; anterior retractor circular, well marked and detached from the adductor. Taxodont dentition only partially observable, showing at least three anterior teeth and four posterior teeth, decreasing in size towards the hinge center. External ornamentation only partially preserved (as seen in specimens L12/C/15 and L12/G/9) composed by wide costae, with visible fine growth lines; interspaces of almost the same width of each single costa.

TABLE 3 HERE

Comparison. The newly recorded *Limopsis* sp. differs from the New Zealand *L. zealandica* Hutton, 1873 and *L. catenata* Suter, 1917 (Beu and Raine 2009) by its wider costa, greater posterior adductor scar and the presence of posterior myophoric ridge.

There are two species under the genus *Limopsis* recorded in the Cape Melville Formation: *L. psimolis* (Anelli et al. 2006) and *L. infericola* (Whittle et al. 2011). *L. psimolis* is big-sized, with almost circular shape, short hinge line and well-marked muscle scars. *L. infericola* is smaller, more oblique and with longer hinge line than *L. psimolis*. The newly recorded taxon is much smaller, its anterior and posterior dorsal lines form an almost straight angle, the adductors are lined up regarding the hinge line and the external ornamentation is much coarser than the other two Melvillean species.

Remarks. The general shape and the presence of inner marginal crenulations resemble *Pectunculina*, previously a distinct genus (Vella 1954) and more recently a subgenus of *Limopsis* (Newell 1969, Oliver 1981, Beu 2006). The new taxon of the Cape Melville Formation is much greater in size than many species assigned to *Pectunculina*, and the presence of marginal crenulations seems to be a variable character in many forms (see discussion of Beu 2006 and Whittle et al. 2011). *Pectunculina* may exhibit some degree of convergence with glycymeridids (Newell 1969, Oliver and Holmes 2006), especially with some *Glycymeris* species. The anterior adductor scar is smaller than the posterior, a character that distinguishes limopsids of glycymeridids. Finally, the lack of preservation of some important features – as resilifer and cardinal area – in all three specimens prevents us from assigning it to a formal new species.

Order LIMIDA Moore, 1952

Superfamily LIMOIDEA Rafinesque, 1815

Family LIMIDAE Rafinesque, 1815

Genus *Limatula* Wood, 1839

Type-species. *Pecten subauriculata* Montagu, 1808

Subgenus *Limatula* (*Antarctolima*) Habe, 1977

Type-species. *Lima* (*Limatula*) *hodgsoni* Smith, 1907

Limatula (Antarctolima) sp. cf. *L. (Antarctolima) ferraziana* Quaglio and Anelli, 2008

Fig. 3

Material. one internal mould of LV with inner layer of the shell partially preserved (P.2702.779).

Locality. P.2702 (locality E of **Fig. 1, Table 2**), Cape Melville Formation, Melville Peninsula, King George Island, West Antarctica.

Description. Internal mould of left valve very small (length, 5mm; height, 6mm); slightly inequilateral, trigonal to ovoid, slightly oblique, equant (elongation = 0.83), moderately inflated; umbones not observed; radial inner sculpture of 16 well developed ribs that barely reach the submargins, and the most posterior and anterior ones forming an angle of 55°, median structure composed by 5th, 6th and 7th (from the anterior) more prominent ridges than others, inner commarginal sculpture of numerous regularly spaced growth lines, extending to auricle area, raised into scale-like ridges when intersecting radial sculpture; dorsal margin short; hinge line almost straight, sizing less than half of shell length (38%), with large triangular resilium; auricles small, almost symmetrical, posterior slightly larger than anterior; ventral margin rounded, slightly crenulated.

Comparison. *Limatula (Antarctolima)* sp. cf. *L. (Antarctolima) ferraziana* differs from the elongated forms found in Cenozoic deposits of Australia and New Zealand (see Buonaiuto 1977, Fleming 1978, Beu and Raine 2009). *Limatula* fossils in Antarctica comprises two occurrences in the Low Head Member of the Polonez Cove Formation, early Oligocene: at Vauréal Peak, from where specimens are assigned to *Limatula (Antarctolima) ferraziana* Quaglio and Anelli, 2008, and at Low Head area (Quaglio et al. 2008). The specimen from the Low Head locality was originally assigned to *Limopsis (Pectunculina)* cf. *insolita* Sowerby, 1846 (Gaździcki and Pugaczewska 1984), while Quaglio et al. (2008) identified it as belonging to *Limatula (Antarctolima)* and Beu (2009) as to *Antarctolima*. *Limatula (Antarctolima)* sp. from the Cape Melville Formation differs from the Oligocene Antarctic *Limatula* by its more trigonal shape, smaller ventral margin and lower number of radial costae. The costae of *Limatula*

(*Antarctolima*) sp. from the Miocene Cape Melville Formation fade in the submargins. Fleming (1978) argued that the external ornamentation of *Limatula* might be useful in taxonomy only in the cases when the radial ribs cease abruptly in the flanks or submargins. However, since the single Melvillean specimen is an internal mould with shell material only partially preserved, it is possible that the ornamentation would extend externally up to the submargins, as observed in modern specimens of *Limatula* (*Antarctolima*) *hodgsoni*. Because of this, the ornamentation pattern of Melville specimen is disregarded of full taxonomical reliability and, thus, we rather designated it as *L. (Antarctolina) ferraziana* under doubt.

Remarks. The genus *Limatula* is currently represented in Antarctica by the subgenus *Antarctolima* and comprises *L. (Antarctolima) hodgsoni*, *L. (Antarctolima) ovalis* (Thiele, 1912) and *L. (Antarctolima) pygmaea*. *L. (Antarctolima) hodgsoni* (Philippi, 1845) occurs in Antarctica and Subantarctic waters, extending to Magellan region, while *L. (Antarctolima) ovalis* is restricted to Antarctic and *L. (Antarctolima) pygmaea* has a Magellan distribution in southern South America (Bouchet and Gofas 2012a). Molecular data suggest a cladogenetic event that occurred at around 19Ma resulted in the speciation of the modern *L. (Antarctolima) ovalis* and *L. (Antarctolima) pygmaea* in Antarctica (Page and Linse 2002). The age estimate is consistent with the Cape Melville Formation age, of around 22Ma (Dingle and Lavelle 1998). *Limatula* sp. from the Cape Melville Formation might have integrated a more diverse group during the early Miocene or even the ancestral stocks that originated the modern, close-related species. Additional better preserved *Limatula* specimens from the Cape Melville Formation would be important not only to clarify the species identification and improve the knowledge on the genus diversity during early Neogene times, but also to confirm the speciation scenario proposed by Page and Linse (2002).

Superorder HETEROCONCHIA Gray, 1854

Clade HETERODONTA Neumayr, 1884

Order PHOLADOMYIDA Newell, 1965

Superfamily THRACIOIDEA Stoliczka, 1870 (1839)

Family PERIPLOMATIDAE Dall, 1895

Genus *Periploma* Schumacher, 1817

Subgenus *P. (Offadesma)* Iredale, 1930

Type-species. *Periploma angasi* Crosse and Fischer, 1864

Discussion. Some authors have argued that *Offadesma* should be considered a separate genus, based on the stronger inequivalve character of the shell, posterior inclined chondrophore and absence of lithodesma in adults (see Griffin and Pastorino 2006, p. 76). Although agreeing with the notion that *Offadesma* forms a very distinctive group, we assume the more conservative classification, in which *Offadesma* is considered a subgenus of *Periploma* (Cox *et al.* 1969). This is based on the fact that an updated systematic revision of the family (or less inclusive groups) is not available (Bouchet *et al.* 2010). Also, the intrinsic preservation bias of most fossil specimens, in which some delicate parts are not observed, makes a detailed taxonomic comparison difficult to be achieved.

Periploma (Offadesma) antarctica sp. nov. Quaglio and Anelli

Figures 4 and 5, Table 4

Diagnosis. Elliptical, inequilateral, with umbones located at around 0.45 of anterior length; anterior dorsal margin short and oblique; rostrum poorly defined, with a narrow gape.

Etymology. Referring to its occurrence, as the first record of the subgenus in Antarctica.

Material. Twenty seven internal molds of conjugated valves and one internal mold of right valve. Holotype: ZPAL L12/B/70; paratypes: all other 30 specimens (ZPAL L12/A/31, L12/B/39-40, L12/B/46-51, L12/B/62-69, L12/B/71-78, L12/B/82, L12/E/1).

Locality. I (Crab Creek; locality D of **Fig. 1, Table 2**), Cape Melville Formation, Melville Peninsula, King George Island, West Antarctica.

Age. Early Miocene.

Description. Shell very thin (as seen in shell fragments close to the hinge), aragonitic. Internal mold large, elliptic, inequilateral, slightly inequivalve; moderately elongate (mean 1.27), compressed (mean 1.83). RV slightly more convex than LV and posterior region of RV more depressed than LV. Umbones elevated above hinge line; beaks opisthogyrous, located at around 0.45 of anterior length; right beak partially superimposing the left beak; umbonal crack of around 10mm, forming a right to oblique angle to the commissure in dorsal view; anterior edge of the crack overlying the posterior. Anteroumbonal ridge narrow and weak; postumbonal ridge broad, well defined, especially in the dorsal region. A faintly defined depression runs from the umbonal region to anterior-ventral margin; a better defined depression is present posteriorly, just behind the postumbonal ridge. Anterior dorsal margin short and oblique; ventral margin rounded; posterior margin slightly elongated and strongly arcuated, faintly curved to the left and with a narrow gape. Chondrophore directed posteriorly, with anterior ventral part deeper than the posterior; clavicle deep, straight at its anterior part and postero-ventrally directed, running from the posterior dorsal end of the chondrophore; anterior secondary ligament partially preserved. Posterior adductor scar small, located postero-dorsally and close to the shell margin. Ornamentation of well-defined growth lines superimposing to form broad undulations (as seen in internal molds).

TABLE 4 HERE

Comparison. *Periploma (Offadesma) antarctica* sp. nov. from the Miocene Cape Melville Formation differs from the middle Eocene *Offadesma marwicki* Fleming, 1950 from Bortonian deposits in North Otago, New Zealand (Fleming 1950), in its less opisthogyrous beaks, more elongate posterior region, more elongate ventral margin, and more closely spaced growth lines and rugae.

Periploma (Offadesma) antarctica sp. nov. differs from *Periploma (Aelga) primaverensis* Griffin, 1991 from the Eocene Río Turbio Formation (Griffin 1991) by its more elliptical shape, slightly longer posterior region, more elongate posterior margin and better defined postumbonal ridge.

Offadesma sp. from middle to late Miocene deposits of New Zealand (Marwick 1931) is externally similar to *Periploma (Offadesma) antarctica* sp. nov., except for the bigger size, and may be conspecific to the new species here described. Although identified in the original work as *Cochlodema* sp., it is more suitable in the *Offadesma* group.

However, the specimen is articulate and the work lacks description and additional figures.

Periploma (Offadesma) antarctica sp. nov. is quite similar to the Patagonian *Offadesma isolatum* Griffin and Pastorino, 2006 from late Miocene Puerto Madryn Formation, Argentina (Griffin and Pastorino 2006). The Antarctic species differs from the Patagonian species by the smaller size, more elongated posterior part of the shell, narrower gape, and shorter and oblique anterior dorsal margins. The Patagonian species is the closest similar to the Antarctic one. Because of the ages and geographical proximity of both species, it would not be surprising if they shared close phylogenetic affinities.

Periploma (Offadesma) antarctica sp. nov. is slightly similar to the Recent *Offadesma angasi* Crosse and Fischer, 1864 that occurs in shallow intertidal beaches of Australia and New Zealand regions (Morton 1981). Miocene species is less inequivalved, more elliptical in shape, the posterior margin is less truncate, the posterior gape is narrower and the posterior dorsal margin is not as arcuate as in the modern species.

Remarks. It seems that the subgenus *Offadesma* had a somewhat cosmopolitan character during the Paleogene-early Neogene times, as it has been recorded in several sites of the Southern Ocean. Apparently it has a strong austral character in its paleobiogeographical evolution along the Cenozoic, which is detached from other Recent periplomatid forms living in the southern South America, as previously pointed out by Griffin and Pastorino (2006). The new species from the Cape Melville Formation corroborates that view and adds Antarctica in the scenario of survival of migrating taxa along southern oceans towards southern South America (Beu et al. 1997, Beu 2009). The cold Circum-Antarctic Current would have been close to its full establishment during Miocene times, but periods of warming would have existed before ice sheets completely covered Antarctica and ice shelves developed around the continent. This oceanographic dynamics may have played an important role in the distribution of this genus in the Neogene.

Paleobiogeography of the Cape Melville Formation bivalves

Genus records, distributions and ecology

The oldest southern *Leionucula* record is from late Cretaceous Santa Marta Formation at James Ross Island, West Antarctica (Strelin et al. 1992), while the oldest record of *Ennucula* is assigned to *Ennucula whatu* Maxwell, 1992, from the late Eocene of South Canterbury, New Zealand (Maxwell 1992). However *Ennucula whatu* is still not listed in Eocene New Zealand species by Beu and Raine (2009). Former nukulid records include a *Nuculoidea* from the late Devonian at Ohio Range, Antarctica (Doumani et al. 1965) and no other nukulid record if found in deposits older than Jurassic (Paleobiology Database, <http://paleodb.org>).

Both genera have a contentious taxonomy. The use of the name *Ennucula* is being replaced for *Leionucula* by some authors to include Cenozoic southern nukulids (Stilwell 1993, 2000, Beu 2009, Beu and Raine 2009, Whittle et al. 2012). The explanation is commonly attributed to that both genera are synonymous and the name *Leionucula* has priority. However, very few studies have discussed the morphological characters supporting this taxonomic decision. Keen (1969) listed only *Leionucula* as a subgenus of *Nucula* as having the external shell surface smooth, resilifer oblique and inner ventral margin smooth. Beu (2009) ascribed nukulids of the Cape Melville Formation to the genus *Leionucula*. On the other hand, Simone (2009) synonymized *Leionucula puelcha* from the middle Miocene of south Argentina (Del Río 1991, 1992) to *Ennucula puelcha*. Stilwell (1993) argued that New Zealand species assigned to *Ennucula* show morphological variations inside the limits of generic variability of *Leionucula*. He also cited Maxwell's (1988) statement that the type-species of *Ennucula* and *Leionucula* are similar in shape and lack of defined sculpture, but the former differs from the latter by having a weaker defined escutcheon and a less well defined anterior area. Beu and Raine (2009) placed the species from late Miocene of New Zealand previously assigned to *Ennucula otamaringaensis* by Beu and Maxwell (1990) in "*Leionucula*" *otamaringaensis*, asserting that it probably belongs to a new nukulid genus. Although Stilwell (1993) stated that the presence of modern *Leionucula* in New Zealand, Spencer et al. (2011) included *Ennucula* – not *Leionucula* – in their nukulid list of New Zealand Economic Zone, while Beu (2009) stated that *Leionucula* still lives in both Antarctica and New Zealand. In New Zealand, *Ennucula* is recorded in two species (*E. strangei* (Adams, 1856) and *E. strangeiformis* (Dell, 1956), Spencer et al. 2011). Nevertheless, their earliest fossil records suggest that both have an early history restricted to the southern oceans. Nukulids are deposit feeders that live in muddy

substrates in a very wide depth ranges, from very shallow to 1000m depth (Bergmans 1978). *Ennucula puelcha* from Magellan Strait was reported from 600m depth (Dell 1964) and other *Ennucula* species from 0m to 3800m depth (EOL 2013).

The oldest records of *Neilo* are from the late Cretaceous Santa Marta Formation on James Ross Island, Antarctica (Strelin et al. 1992) and from the late Cretaceous Lefipán Formation at Chubut, Argentina (Paleobiology Database, www.paleodb.org). Although recorded in further southern Cenozoic records, species of the genus currently live only in New Zealand waters (Spencer et al. 2011). Miocene was the time interval when it was mostly widespread, being recorded in Antarctica (Anelli et al. 2006), Argentina (Malumian et al. 1978), Chile (Frassinetti and Covacevich 1999) and New Zealand (Beu and Maxwell 1990). Modern species of *Neilo* are infaunal suspension feeders that commonly thrive in poorly oxygenated muddy bottoms in depths ranging from 7m to 100m (Marshall 1978).

Panopea is a cosmopolitan genus with oldest record assigned to Triassic of Siberia (Paleobiology Database, www.paleodb.org). The genus is widespread since Cretaceous, including many southern records (Paleobiology Database, www.paleodb.org), but it is currently absent in Antarctica (Gofas 2012b). The modern northern *Panopea* (*P. abrupta*) is a suspension feeder that occurs in muddy to sandy substrata in shallow subtidal depths to 110m (Goodwin and Pease 1991).

Periploma shows a northern widespread distribution since the Cretaceous (Paleobiology Database, www.paleodb.org), and is recorded in Paleocene deposits of Antarctica and Argentina (see "Paleontology" section). Presently it is found worldwide, except for Antarctic waters (Bouchet 2013). Modern representatives are infaunal suspension feeders in muddy to sandy substrates (Morton 1981).

Although with unpublished oldest records in Jurassic of France, Germany and Hungary, the genus *Limopsis* was globally widespread since the Cretaceous (Paleobiology Database, www.paleodb.org, see "Paleontology" section), and is presently cosmopolitan, including Antarctic and Subantarctic waters (Bouchet and Gofas 2012b). Reported living species include depths of 600m in Australia (Lamprell and Healy 1998), 422m to 1280m in New Zealand (Beu 2006), and from shallow to 4678m in Antarctic and subantarctic (Griffiths et al. 2003).

The oldest *Limatula* record is from the late Carboniferous of Oklahoma, North America (Girty 1915). The oldest southern record is from Jurassic of New Zealand

(MacFarlan 1998). During Cretaceous, the genus was already widespread, including southern records in Antarctica (Strelin et al. 1992) and New Zealand (Warren and Speden 1977). Currently, more than 80 species are distributed in all oceans, including Antarctica and Subantarctic waters (Bouchet and Gofas 2012a). *Limatula* species are free-lying suspension feeders living from shallow to deep-waters (Fleming 1978, Allen 2004). High densities of Antarctic species occur from 6 to 695m on hard substrata, gravel or on mat formed by sponge spicules (Nicol 1966, Dell 1990).

The genus *Yoldia* is formerly recorded in the late Carboniferous of Oklahoma, North America (Girty 1915). Younger records are from the North America (Paleobiology Database, www.paleodb.org) and it appears in the South Hemisphere during Cretaceous, including late Cretaceous of New Zealand (Warren and Speden 1977). It attains a somewhat cosmopolitan character in the Cretaceous, but the greatest distribution is achieved after the Miocene up to Recent (Paleobiology Database, www.paleodb.org; Bouchet and Gofas 2012c). The modern Antarctic species *Yoldia eightsi* is a shallow deposit feeder, and occasionally shallow infaunal suspension feeder (Davenport 1988) of soft sediments from 4m to 824m depth, being more commonly found in depths shallower than 100m (Dell 1990).

The genus *Antarctipecten* was recently erected by Beu and Taviani (2013) to include Antarctic scallops with no or very few radial macrosculpture of plicae previously assigned to *Adamussium alanbeui* (Jonkers, 2003). The Family Pectinidae has a Cenozoic history in Antarctica that initiated in the mid-Paleogene, with the unconstrained records of “*Chlamys*” sp. A and B in the early Eocene La Meseta Formation (Stilwell and Zinsmeister 1992). However, “*Chlamys*” sp. A was assigned to the limid *Acesta* (*Antarcticesta*) *laticostata* Stilwell and Gaździcki, 1998 by Beu (2009). Apart of this, each pectinid genus with some record in Antarctica has a restricted history in the southern oceans during the Cenozoic. The longest record is of *Austrochlamys*, from the early Miocene of East Antarctica (Beu and Taviani 2013), late Miocene to early Pliocene of West and East Antarctica (Jonkers 2003), late Pleistocene of Falkland Islands and around New Zealand (Jonkers 2003), as well as modern records around southern South America (Beu and Taviani 2013). *Zygochlamys* Ihering, 1907 occurs from the late Eocene to Pliocene, but its distribution is restricted to South America (Jonkers 2003). *Ruthipecten* Beu and Taviani, 2013 occurs in the late Miocene of East Antarctica (Beu and Taviani 2013). *Psychrochlamys* Jonkers, 2003 is recorded in Pliocene to Recent waters of Chile, Falkland Islands and New Zealand (Jonkers 2003).

Adamussium Thiele, 1934 has the oldest record in the early Oligocene (Jonkers 2003, Quaglio et al. 2008), but it has a rather continuous record until Recent, as it is found in the late Oligocene of West Antarctica (Quaglio et al. 2010), late Miocene of East Antarctica (Stilwell et al. 2002), early Pliocene of West Antarctica (Jonkers 2003), Pleistocene of East Antarctica (Jonkers 2003) and in modern waters around Antarctica (Schiaparelli and Linse 2006).

Distributional patterns

Panbiogeographic analysis shows two main distributional patterns of genera recorded in the Cape Melville Formation (**Fig. 6**). Roughly all taxa show the oldest records in the high latitudes of the Southern Hemisphere during Cretaceous and are recorded along the Cenozoic. The exceptions are *Ennucula*, with the oldest record in the Eocene of New Zealand, and *Antarctipecten*, earliest recorded in the Oligocene of Antarctica. Also, all genera – except for *Antarctipecten* – have modern representatives. The main difference occurs with records after Miocene and Pliocene: some genera persisted widespread in the present, while others became extinct in Antarctica after Neogene (**Fig. 6**).

FIGURE 6 HERE

The cluster analysis (**Fig. 7**) shows two main groups: one clustering *Ennucula*, *Yoldia* and *Antarctipecten* and other grouping the remained genera. Both *Yoldia* and *Antarctipecten* records are scarce, which would explain their clustering with *Ennucula* with the smallest similarity. *Ennucula* and *Leionucula* group with different groups probably because fossil record of *Ennucula* is younger than the group *Leionucula* belongs to.

Ennucula and *Leionucula* show a somewhat complementary pattern in the panbiogeography, being *Leionucula* recorded since the late Cretaceous to Pliocene and Recent, and *Ennucula* from the early Miocene to Recent (**Fig. 6A**). Both distributions overlap during Oligocene, Miocene and Pliocene times. However, none of both genera are recorded in the same locality, except for the Recent, when both genera are recorded in Australia, and for the Miocene, when both *Ennucula* (Anelli et al. 2006) and *Leionucula* (Whittle et al. 2012) occur in the Cape Melville Formation.

Limopsis and *Limatula* are widespread both in and out of Antarctica along the Cenozoic up to Recent (**Fig. 6B**). Although the fossil record of *Yoldia* is scarce, its pattern is similar to *Limopsis* and *Limatula*, except for its limited record in New Zealand (**Fig. 6B**).

Antarctipecten is restricted to both West and East Antarctica in Early Oligocene and Early Miocene (**Fig. 6B**) and is one of the many pectinid taxa originated in southern oceans during the Cenozoic that went to extinction in the Neogene.

Apart of *Limopsis* and *Limatula*, panbiogeographic pattern (**Fig. 6**) is confirmed by the cluster result (**Fig. 7**). *Neilo* and *Panopea* share more similar records and represent, together with *Leionucula* and *Periploma*, the group with oldest fossil record present in Antarctic and Subantarctic that became restricted to Subantarctic after Miocene and Pliocene. Conversely, *Limopsis* and *Limatula* share the same pattern of old fossil records which remained in Antarctica and Subantarctic up to the Recent.

FIGURE 7 HERE

Discussion

The biogeographical history of bivalve genera recorded in the Cape Melville Formation indicates that they are composed mostly by cosmopolitan taxa with old ancestrality (Beu 2009), except for *Antarctipecten*. Modern representatives comprise highly diverse genera with several species living in Subantarctic and/or Antarctic waters.

The almost complementary panbiogeographic distribution of genera *Ennucula* and *Leionucula* might reflect the taxonomic problems previously pointed out by several authors (Stilwell 1993, 2000, Beu 2009, Beu and Raine 2009, Whittle et al. 2012), and may be one evidence of synonymy. Regarding both *Ennucula* and *Leionucula* as a single genus, its distribution would fit to patterns displayed by *Neilo*, *Panopea* and *Periploma*, which were widespread in the southern oceans up to Miocene and Pliocene times, eventually becoming restricted to Subantarctic regions (**Fig. 6A**).

The glacial episodes along the Cenozoic may have affected the distribution of southern bivalves as previously suggested (e.g., Zinsmeister 1979, Beu et al. 1997, Crame 1999, Jonkers 2003, Quaglio et al. 2008, Beu 2009, Krug et al. 2010, Whittle et al. 2011). The glacial mechanisms that influenced the bivalve distributions would have been by means of the temperature drop itself and ice scour during ice-shelf advance.

One important aspect to note is that the fossil record of the Cape Melville genera that were extinct extends to the Miocene or Pliocene in Antarctica (see **Fig. 6**). Hence, they were extinct after the early Miocene and/or Pliocene. In another words, it seems impossible that the glacial events occurred at the end of Paleogene and most part of Neogene caused their extinctions. Instead, they may be related to glacial events occurred in the Plio-Pleistocene (Raymo et al. 2006).

The early Miocene experienced a dynamic ice growth and retreat together with oscillation in bottom water temperatures (Pekar and DeConto 2006). Hence, the early Miocene was a time of unfavorable conditions to stenotopic taxa of restricted temperature and bathymetric preferences. Most bivalves of the Cape Melville Formation include some genera with species currently occurring in temperate to warm seas (as *Yoldia*, *Limatula* and *Limopsis*). Most of them are cosmopolitan and, thus, belonging to lineages able to adapt to several environmental conditions. The drop in temperature would be a primer explanation for the extinction of *Neilo* and maybe *Antarctipecten* from Antarctica. However, this plea seems to be unjustifiable to explain the extinction of *Panopea*, since extant members of this genus are flourishing in the Present-day high northern latitudes. Although *Limatula* and *Yoldia* species currently live in platformal areas, they extend their bathymetric distributions to deep depths. The only exclusive shelfal genera – *Neilo*, *Panopea* and, perhaps, *Antarctipecten* – are restricted to Subantarctic or northern areas as southern South America, New Zealand and Australia. Hence, the reduction of shelf areas after ice shelf expansion during the Plio-Pleistocene (Raymo et al. 2006) is the best explanation to the paleobiogeographical dynamics of the genera recorded in the Cape Melville Formation. Indeed, living modern truly polar molluscs are recorded only after Oligocene, and near-shore taxa are restricted to Subantarctic areas (Beu 2009).

Berkman et al. (2004) interpreted the disappearance of pectinids from Antarctica as consequence of coastal areas limitation that would have started after Oligocene and intensified after Pliocene. Three of all six scallop genera recorded in Cenozoic deposits of Antarctica have modern southern representatives, but only *Adamussium colbecki* still lives in Antarctica. Almost all pectinids were prevented from thriving in Antarctic due to ice shelf expansion, with *Adamussium* being the only form able to live under ice covering in habitats similar to deep-water ('polar emergence' of Berkman et al. 2004).

The Early Miocene of East Antarctica (ANDRILL-2/2A drill core; see Beu and Taviani 2013) seems to be the latest record of high pectinid diversity in Antarctica.

Final Remarks

Although the advance of ice shelves would not necessarily be the explanation to all bivalves that went extinct from Antarctica, it may be the cause to justify the extinction of those Cape Melville genera from Antarctic waters. It would have occurred after early Miocene or early Pliocene, and not along the Cenozoic. More specifically, it would have occurred after the Plio-Pleistocene glaciation event, which resulted in the expansion of ice shelves in Antarctica (Raymo et al. 2006). The extinction of some genera recorded in the Cape Melville Formation occurred by means of limitation of coastal areas to shallow and shelf bivalves to thrive as consequence of the ice shelf expansion. Although this scenario was proposed Berkman et al. (2004, but see Beu 2009), it was previously linked to the long-term Cenozoic glacial history of Antarctica. Our data indicate that it occurred only after the extensive glaciation in Plio-Pleistocene. Those genera currently living in the Antarctic are highly diverse, with several species thriving also in Antarctic periphery. On the other hand, exclusive Subantarctic genera have much lower species richness and represent relict taxa that formerly were widespread in Cenozoic southern oceans.

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TABLES

Table 1. Invertebrate macrofossils recorded in the Cape Melville Formation (Miocene) at Melville Peninsula, King George Island, Antarctica. Localities A-M are shown in figure 1.

Locality in figure 1	Locality in original work	Recorded fossils	Reference
A	194	Scleractinian (<i>Flabellum</i>)	Roniewicz & Morycowa 1987
	193		
B	Lava Crag	Bivalves (<i>Neilo</i> , <i>Panopea</i>)	Anelli <i>et al.</i> 2006
C	P.2701	Decapoda (<i>Hoploparia</i>)	Feldmann & Crame 1998
D	187, I, Crab Creek	Scleractinian (<i>Flabellum</i>)	Roniewicz & Morycowa 1987
		Polychaete jaws	Szaniawski & Wrona 1987
		Gastropods	Karczewski 1987
		Echinoids	Jesionek-Szymańska 1987
		Homolodromiid crab (<i>Antarctidromia</i>)	Förster <i>et al.</i> 1987
		Bivalves (<i>Periploma</i>)	this work
	Hard Ground	Bivalves (<i>Ennucula</i> , <i>Limopsis</i> , <i>Periploma</i>)	Anelli <i>et al.</i> 2006
E	186 (II)	Scleractinian (<i>Flabellum</i>)	Roniewicz & Morycowa 1987
	II	Polychaete jaws	Szaniawski & Wrona 1987
		Gastropods	Karczewski 1987
		Echinoids	Jesionek-Szymańska 1987
		Bivalves (<i>Leionucula</i> , <i>Limopsis</i> , <i>Limatula</i> , <i>Antarctipecten</i>)	Jonkers 2003, Whittle <i>et al.</i> 2011, Whittle <i>et al.</i> 2012, Beu & Taviani 2013, this work
	P.2702	Decapoda (<i>Hoploparia</i>)	Feldmann & Crame 1998
		Brachiopods (<i>Lyothyrella</i> , <i>Paraldingia</i>)	Bitner & Crame 2002
		Bryozoans (<i>Aspidostoma</i>)	Hara & Crame 2004
	P.2707	Bivalves (<i>Leionucula</i>)	Whittle <i>et al.</i> 2012
F	185	Scleractinian (<i>Flabellum</i>)	Roniewicz & Morycowa 1987
G	184	Scleractinian (<i>Flabellum</i>)	Roniewicz & Morycowa 1987
I	Chamney	Bivalves (<i>Neilo</i> , <i>Panopea</i>)	Anelli <i>et al.</i> 2006
J	III (Grzyb)	Polychaete jaws	Szaniawski & Wrona 1987
		Gastropods	Karczewski 1987
		Bivalves (<i>Limopsis</i>)	this work
K	182	Scleractinian (<i>Flabellum</i>)	Roniewicz & Morycowa 1987
	V (Kamień)	Gastropods	Karczewski 1987
		Bivalves (<i>Limopsis</i>)	this work
L	IV (East)	Polychaete jaws	Szaniawski & Wrona 1987
		Gastropods	Karczewski 1987
		Bivalves (<i>Limopsis</i>)	this work
M	Penguin Rookery	Bivalves (<i>Ennucula</i> , <i>Yoldia</i>)	Anelli <i>et al.</i> 2006
	VI	Gastropods	Karczewski 1987

Table 2. Bivalve species recorded in the Cape Melville Formation. Site locations are detailed in the **figure 1B-C**.

Family	Species	Site	Description
Nuculidae	<i>Ennucula frigida</i>	D	Anelli <i>et al.</i> 2006
	<i>Ennucula musculosa</i>	M	Anelli <i>et al.</i> 2006
	<i>Leionucula melvilleana</i>	E, F	Whittle <i>et al.</i> 2012
Malletiidae	<i>Neilo rongelii</i>	B, I	Anelli <i>et al.</i> 2006
Sareptidae	<i>Yoldia peninsularis</i>	M	Anelli <i>et al.</i> 2006
Limopsidae	<i>Limopsis psimolis</i>	D	Anelli <i>et al.</i> 2006
	<i>Limopsis infericola</i>	E	Whittle <i>et al.</i> 2011
	<i>Limopsis</i> sp.	J, K, L	this work
Limidae	<i>Limatula</i> sp. cf. <i>L. (Antarctolima) ferraziana</i>	E	this work
Pectinidae	<i>Antarctipecten alanbeui</i>	E	Beu and Taviani 2013
Hiatellidae	<i>Panopea (Panopea)</i> sp. cf. <i>P. regularis</i>	B, I	Anelli <i>et al.</i> 2006
Periplomatidae	<i>Periploma acuta</i>	D	Anelli <i>et al.</i> 2006
	<i>Periploma (Offadesma) antarctica</i> sp. nov.	D	this work

Table 3. Measurements (in mm) of representative specimens of *Limopsis* sp. from the early Miocene Cape Melville Formation, Melville Peninsula, King George Island, West Antarctica.

Specimen	Type	Height	Length	Width	Elongation	Obesity
L12/A/30	IM, AV	20.8	21.2	11	1.02	1.89
L12/C/15	IM, AV	23.5	26.3	14.3	1.12	1.64
L12/G/9	IM, RV	17.3	20.2	8.8*	1.17	1.92
Mean		20.5	22.6	11.4	1.10	1.82

*Approximated measurement

Table 4. Measurements (in mm) of representative specimens of *Periploma* (*Offadesma*) *antarctica* sp. nov. from the early Miocene Cape Melville Formation, Melville Peninsula, King George Island, West Antarctica.

Specimen	Type	Height	Length	Width	Elongation	Obesity
L12/A/31	IM, AV	40.9	48.9	19.8	1.20	2.07
L12/B/39	IM, AV	33.2	43.6**	18.5	1.31	1.79
L12/B/40	IM, AV	29.4	37.8*	15.5	1.29	1.90
L12/B/46	IM, AV	37	47.9*	20	1.29	1.85
L12/B/49	IM, AV	33.4	44.2*	18.4	1.32	1.82
L12/B/50	IM, AV	33.3	42.3*	17.4	1.27	1.91
L12/B/51	IM, AV	37.3	42.1*	18	1.13	2.07
L12/B/62	IM, AV	37.8	46*	18.1	1.22	2.09
L12/B/63	IM, AV	39.6	54.3*	23.5	1.37	1.69
L12/B/64	IM, AV	29.8	36.7*	16	1.23	1.86
L12/B/65	IM, AV	37.9	47*	21.2	1.24	1.79
L12/B/66	IM, AV	31.5	47.4*	17.9	1.50	1.76
L12/B/67	IM, AV	33	42.3**	20.9	1.28	1.58
L12/B/70	IM, AV	43.5	60.3	25.7	1.39	1.69
L12/B/71	IM, AV	45.4	57.4*	25	1.26	1.82
L12/B/72	IM, AV	40	46.9	22.1	1.17	1.81
L12/B/73	IM, AV	37.8	54.3	20.6	1.44	1.83
L12/B/74	IM, AV	36.4	49.4*	21.3	1.36	1.71
L12/B/75	IM, AV	34.9	46*	17.4	1.32	2.01
L12/B/76	IM, AV	34.6	42.2*	21.4	1.22	1.62
L12/B/77	IM, AV	35	40.1*	20.4	1.15	1.72
L12/B/78	IM, AV	27.7	34.7*	17.9	1.25	1.55
L12/B/82	IM, AV	36.4	44	18.1	1.21	2.01
L12/E/1	IM, AV	34.8	45.5*	20.6	1.31	1.69
Mean		35.9	45.9	19.8	1.3	1.8

*Specimen with partially broken margin; minimal measurement error

**Specimen with anterior or posterior region broken; approximated measurement

FIGURES

Figure 1. The Cape Melville Formation geology and fossil sites. **A**, Location map of the Melville Peninsula at King George Island, West Antarctica. **B**, Geological map of Melville Peninsula showing the sites of recorded fossils. **C**, Bivalve species recorded from sites A-M; key to occurrences of other groups in Table X. (Bivalve data from Jonkers 2003, Anelli et al. 2006, Whittle et al. 2011, 2012, Beu and Taviani 2013. Occurrences of other groups from Föster et al. 1987, Jesionek-Szymańska 1987, Karczewski 1987, Roniewicz and Morycowa 1987, Szaniawski and Wrona 1987, Feldmann and Crame 1998, Bitner and Crame 2002, Hara and Crame 2004).

Figure 2. *Limopsis* (*Pectunculina*) sp. from Cape Melville Formation, Melville Peninsula, King George Island, Antarctica. **A-F**, internal mould (L12/A/30); **A**, left view; **B**, draw of **A** showing adductor scars and inner ornamentation; **C**, right view; **D**, dorsal view; **E**, latex cast of dorsal with draw showing partially preserved hinge features; **F**, ventral view. **G-J**, internal mould with partial shell preserved (L12/C/15); **G**, right view; **H**, draw of **G** showing muscle scars; **I**, left view; **J**, dorsal view. **K-L**, internal mould (L12/G/9); **K**, right view; **L**, draw of **K** showing muscle scars and shell remains; **M-N**, plasticine cast of **K**; **M**, right view; **N**, draw of **M** showing muscle scars and shell remains. Symbols: **aa**, anterior adductor scar; **ar**, anterior pedal retractor scar. Scale 10mm.

Figure 3. *Limatula* (*Antarctolima*) sp. cf. *L. (Antarctolima) ferraziana* from Cape Melville Formation, Melville Peninsula, King George Island, Antarctica. **A-B**, internal mould with remains of shell material (P. 2702.779). **A**, with no coating, showing shell remains; **B**, coated with ammonium chloride. Scale 5mm.

Figure 4. *Periploma (Offadesma) antarctica* sp. nov. from the early Miocene Cape Melville Formation, King George Island, West Antarctica. **A-E**, holotype (L12/B/70), internal mold; **A**, left view; **B**, drawing of **A** showing bivalve features; **C**, right view; **D**, dorsal view; **E**, ventral view. **F-K**, paratype (L12/B/72), internal mold; **F**, left view; **G**, right view; **H**, dorsal view; **I** ventral view; **J**, anterior view; **K**, posterior view. **L**, paratype (L12/B/46), internal mold in left view; **M**, drawing of **L** showing bivalve features. Symbols: **pa**, posterior adductor scar; **pg**, pedal gape; **uc**, umbonal crack. Scale 10mm.

Figure 5. Serial sections of left valve of *Periploma* (*Offadesma*) *antarctica* sp. nov. (L12/E/1), showing the chondrophore (**cd**) and the anterior part of the clavicle (**cl**). Note the posteriorly and downwardly directed chondrophore and the deep clavicle. Numbers represent distance in mm of the section to the commissure plane: as minor the number as closer to the right valve commissure.

FERNANDA QUAGLIO, HUW GRIFFITHS, KATRIN LINSE, ROWAN J. WHITTLE, SILVIO NIHEI & MARCELLO G. SIMÕES. Broken apart and frozen out: the fate of the Cenozoic southern marine fauna. *Em preparação.*

BROKEN APART AND FROZEN OUT: THE FATE OF THE CENOZOIC SOUTHERN MARINE FAUNA

Abstract

Using the Bivalvia as a model taxon, this study shows that the present day Southern Hemisphere marine biogeographic provinces were shaped during the Cenozoic due to a combination of environmental changes. Distinct paleobiogeographic provinces originating in the Early Paleogene became increasingly pronounced following a series of events including tectonic isolation, formation of the Antarctic Circumpolar Current and the associated climatic cooling and glaciation. Increases and decreases in faunal similarity levels across the Southern Hemisphere during the Cenozoic significantly correlate with global temperature trends, and the chronological order of Gondwana breakup. Analysis of faunal similarity and temperature curves indicate that cooling increased the endemism of the Southern Ocean fauna. These results have implications for a less unique Antarctic marine fauna in a potentially warmer future world.

Keywords: Paleobiogeography, bivalves, Antarctica, Cenozoic, Antarctic isolation, fossil

The Southern Hemisphere experienced profound environmental change during the Cenozoic due to plate tectonics and changes to oceanographic, climatic and atmospheric circulation. Early Cenozoic climatic changes included the Paleocene-Eocene Thermal Maximum (PETM), a geologically short period of rapid global warming at around 55 Ma thought to have been caused by the sudden input of large volumes of greenhouse gases into the atmosphere raising global temperatures by ~6°C over 20,000 years (Katz et al., 1999).

Major tectonic changes included the opening of the Tasmanian Gateway after Australia and Antarctica separated in the Late Eocene to Early Oligocene (Exon *et al.* 2004, Stickley *et al.* 2004). Similarly, the Drake Passage formed after the break-up of Antarctica and South America during the Late Eocene (Scher and Martin 2006) to late Early Oligocene (Barker and Thomas 2004). These are believed to be key deep Southern Ocean gateways (Crame 1999) and are tied to the origin of the Antarctic Circumpolar Current (ACC), in the Late Eocene (Lawver and Gahagan 2003) to the Late Oligocene (Lyle *et al.* 2007). Both cooling and opening of oceanic gateways shaped the biotic evolution of the southern regions throughout the Cenozoic to the Present-day (Beu *et al.* 1997).

Climatic evidence, from oxygen isotopic data, points to a global cooling (Zachos *et al.* 2001, Liu *et al.* 2009) and the development of the Antarctic ice sheet (Coxall *et al.* 2005) at the Eocene/Oligocene boundary (Lear *et al.* 2008). The main triggering mechanism is thought to be linked to a variety of factors, such as: the reorganization of marine and atmospheric currents; the complete tectonic isolation of Antarctica from Australia and South America (Kennett 1977); an abrupt decrease of atmospheric CO₂ along a temperature threshold (Pagani *et al.* 2011); and a drop in CO₂ during times of orbitally-induced decline in the polar seasonality (DeConto and Pollard 2003).

Modern terrestrial biotas from Antarctica show evolutionary histories linked to early Cenozoic or even late Mesozoic events (Convey and Stevens 2007) mainly as a consequence of tectonic changes through time. Seismic data and fossil floral composition records from drillholes around the Antarctic Peninsula suggest that the truly polar cold conditions (“cold polythermal”) were achieved only after the Middle Miocene, along with the development the ice sheet (Anderson *et al.* 2011). Unlike their terrestrial counterparts which were increasingly isolated by these oceanic gateways,

marine groups might reflect both tectonic and oceanographic connectivity and changes. There have been studies of marine microfossils linked to climate change in the Cenozoic but less is known about high latitude macrofossil groups (Clarke & Crame, 1992). Bivalvia are a good macrofossil model taxon for analyzing faunal patterns through the Cenozoic as they are the most abundant macrofossil group found from Antarctica and their records include many key periods of environmental change. The Cenozoic paleobiogeography of southern marine invertebrates remains unconstrained (Crame 1999, Beu 2009), and previous studies have not employed any statistical or biogeographical methods over a comprehensive dataset encompassing an entire class of marine animals.

Understanding how southern marine molluscs responded to environmental change through the Cenozoic is a key issue to address future environmental change in the Southern Ocean and its impact on marine invertebrates.

Over 41,000 bivalve records from five Southern Hemisphere regions (Antarctica, South America, South Africa, Australia and New Zealand) from all major epochs from the last stage of the Cretaceous (~70 Mya) to the Recent were analyzed at genus level. Paleobiogeographic relationships were measured to assess how distributional patterns of the bivalves evolved following environmental changes that occurred during the Cenozoic. These results are important for understanding how modern faunal distributions may respond to future climate change.

Background: The Cenozoic fossil record

The fossil record of molluscs from Cretaceous and Cenozoic deposits suggests the existence of a huge paleobiogeographic province from the Cretaceous to the Eocene, (Zinsmeister 1979a, b) prior to the extensive, perennial Antarctic glaciation. This

“Weddellian Province” encompassed southern Australia, Antarctica, New Zealand and southern South America (Zinsmeister 1979a). Overall, the faunal composition of the Cretaceous to Eocene record of Antarctic bivalves indicated mild climates (Stilwell and Zinsmeister 1992), with a high affinity to cosmopolitan and Subantarctic modern genera (“anti-glacial” character, Beu 2009). Oligocene deposits recorded the first truly polar bivalve representatives at genus level (such as the pectinid *Adamussium*) and many of them are still living in Antarctica and the Southern Ocean (Gazdzicki and Pugaczewska 1984, Jonkers 2003, Quaglio *et al.* 2008, 2010, Beu 2009, Whittle *et al.* 2012). For other molluscs, however, the oldest records of genus representatives of species presently living in Antarctica are traced back to the Paleocene and Eocene (see Crame 2013 for examples on neogastropods). Extensive glaciations after the Paleogene on the continent are followed by the extinction of more derived families in Antarctica (such as Corbulidae, Mactridae, Veneridae, Ostreidae, Glycymerididae, Cucullaeidae), as consequence of ecological niche reduction due to cooling temperatures (Krug *et al.* 2010). As a rule, present-day near-shore taxa became restricted to Subantarctic areas (Beu 2009).

Paleobiogeographic pattern

The faunal similarities at genus level, using two different methodologies, between the different geographic areas at different time periods during the Cenozoic are displayed in figure 1. The results show a range of patterns from long-term geographic isolation to widely shared faunas due to similar environmental conditions or fewer barriers to dispersal. The data divides into two well supported clades; an ‘old’ group (grey box encompassing the Cretaceous and Paleocene) and a ‘young’ group (yellow box, Eocene and younger) (Fig.1). The “old” group includes the Cretaceous of all areas

and the Paleocene of Antarctica, South America and Australia. The major exception is the New Zealand Paleocene, which groups with all “young” New Zealand time periods (orange box, Fig. 1).

The New Zealand group branches with the younger Australian intervals and the Recent South Africa. New Zealand Paleocene to Recent forms a single palaeogeographic area indicating that the biota was continuous and distinct from other geographic areas throughout an expanded time-range. The exact position of the Australian Miocene differs between the two methods used. Other than that, both methods suggest that Australia and New Zealand show a greater generic level similarity through the Cenozoic than they do to Antarctica or South America. The Pliocene and Pleistocene of South Africa belong to a separate group and the positions of the Miocene South Africa and Pliocene Australia differ between the two methodologies.

Antarctic and South American time slices after the Eocene form a more closely-related group than any other region or time interval (pale lilac box, Fig. 1). Within this younger Antarctic/South American grouping the majority of sub-divisions occur by geographic area, therefore, indicating a degree of faunal distinctness with some shared elements between the two continents. The significant exception to this pattern is the grouping of the Recent Antarctic and Recent South American faunas on a distinct branch. This indicates that the level of faunal similarity is greater between the two continents at the present day than it is between either geographic area at any other time period. It is also important to note that the Recent Antarctic-South American clade/cluster groups more closely with the young South American grouping than with the other young Antarctic groupings. One possible explanation for this could be the fact that the data for the Recent is better constrained than the fossil record. This also would

explain the poorly constrained placement of the Pleistocene of Antarctica in the Cluster analysis.

Although there are some differences between the two methodologies used as to the exact position of some key time periods, the overall splits between the “old” and “young” and the Australasian and Antarctic/South American groupings are evident. The key difference between the Cluster and PAE methods is the position of the Antarctic Eocene. The Cluster result loosely groups this period with the Eocene to Miocene South America, while the PAE cladogram groups the Eocene to Pliocene of Antarctica in the same clade, indicating different faunal identities for South America and Antarctica from the beginning of the Eocene. However, with the cluster grouping cut-off point of 28%, the Antarctic Eocene is only part of the Oligocene to Recent Antarctic and South American group (pale lilac box, fig. 1), and shows no clustering to any of other more defined group.

Environmental Drivers

The biogeographic dynamics, shown in Figure 2, are a result of the main environmental changes which occurred during the Cenozoic (paleogeographic reorganization and changes to climate, and oceanic circulation).

The temporal clade formed by all regions in the Cretaceous, and some in the Paleocene reflects both the recovery following the K/Pg mass extinction event and the final break-up of East Gondwana. It also supports the existence of Weddellian Province (Zinsmeister 1979a, b). The tectonic drift of New Zealand from Antarctica started at around 84Ma (Storey et al. 1999), the resulting overall faunal similarity decrease is seen by the early differentiation of the New Zealand fauna following the end of the Cretaceous. Therefore, the Southern Hemisphere marine fauna that was once part of a

single paleobiogeographic province (the Weddellian Province) would have separated as early as the Paleocene and not in the Eocene as previously suggested (Zinsmeister 1979b). Overall faunal similarity increased during the rapid warming of the PETM in the Early Eocene. The land masses of Australia and Antarctica separated during the Eocene to Oligocene (Exon et al. 2004, Stickley et al. 2004), which caused a decline in global temperatures (Zachos et al., 2001, 2008) and in the numbers of shared bivalve taxa.

The time period around the Eocene-Oligocene boundary is associated with great faunal changes including changes to the composition of molluscan assemblages and a reduction in durophagous predators such as sharks, rays and crabs (Stilwell and Zinsmeister 1992, Aronson et al. 2007). These changes have been linked to the final tectonic separation of Antarctica (Barker and Thomas 2004, Scher and Martin 2006) and South America leading to the onset of Antarctic cooling (Coxall et al. 2005, Lear et al. 2008) and the formation of the ACC. This is seen in our data by the clear geographical differentiation of faunal provinces and a subsequent drop in overall similarity.

Antarctica and southern South America formed different, but closely related provinces, at least from the Eocene to Pliocene, and they are presently much more similar than they were during Paleogene-Neogene times. Also, a group formed by the Australian young intervals (Pleistocene and Recent) and Recent of South Africa suggests that both regions share more bivalve genera in the late Neogene than the Recent South Africa does with its older time-intervals. The paucity of data from South Africa might be responsible for this grouping. However, Recent oceanographic configuration might explain the similarity between Recent Australia and South Africa. The Subtropical Front ranges from southern South Africa to part of the west and

southwestern coasts of Australia (UNESCO 2009). Although bivalves are benthic for the majority of their lives, many species have pelagic larvae, enabling a wide dispersal (Scheltema 1977).

We compared the cumulative similarity curve of the five areas to the oxygen-isotopic paleotemperature curve (Zachos *et al.* 2001) (Figure 2). Both curves follow a similar trend throughout the Cenozoic. The higher the temperature, the higher the similarity, and the lower the temperature, the lower the similarity (linear polynomial regression correlation, $R^2 = 0.645$, $P = 0.0003$). The five areas became more and more climatically heterogeneous through the Cenozoic. The climate cooling and associated glaciation increased the distinctness of each region's faunal composition, especially that of the Antarctic. This increased distinctness is due to a decrease in Southern Ocean temperatures leading a selection for cold tolerant taxa around Antarctica (Aronson *et al.*, 2007). Cooling and geographic isolation resulted in an increase in endemism, which is reflected by decreasing overall faunal similarity. The similarity and temperature curves appear to decouple in the Miocene. However, this is likely to be a reflection of a lack of data from the Early Miocene fossil records of South Africa and Antarctica, decreasing the overall similarity of the five regions.

From the Pleistocene to Recent faunal similarity increases, while recorded temperatures are at their lowest in the curve. This might be because the number of taxa shared between Antarctica and South America increases from the Pliocene to Recent. The rise in the similarity between these regions after the Plio-Pleistocene might reflect oceanographic changes occurred in this time interval. However, this may also partly reflect the higher number of known genera recorded from the Recent in all regions when compared to the fossil record.

Conclusions

We conclude that major environmental events are the key drivers in shaping the biogeographic relationships in the Southern Hemisphere throughout the Cenozoic Era. The combined effects of these interlinked environmental changes such as tectonic separation and climate change, as represented by the temperature curve (Zachos et al., 2001), are clearly mirrored by the degree of faunal similarity between the geographic regions. These results have significant implications for a less unique Antarctic marine fauna in a potentially warmer future world.

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Figure 1. Palaeogeographic relationships of the bivalve genera in the Southern Hemisphere during the Cenozoic.

Cluster analysis (left) and parsimony analysis of endemicity (PAE, right) based on record of 908 bivalve genera in Antarctica, southern South America, South Africa, Australia and New Zealand from Cretaceous to Recent. Coloured boxes represent the major splits in the Cluster analysis with a cut off of 28% similarity for the main paleobiogeographic groupings (darker shades). Dotted lines indicate clades/groups with no agreement between Cluster and PAE analyses.

Figure 2. A graphical representation of the spatial and temporal Palaeogeographic relationships displayed against the overall similarity between all regions and the Zachos (2001) temperature reconstruction.

Compilation of results on multivariate analysis and parsimony analysis of endemism of bivalve genera from the Southern Hemisphere, Cretaceous to Recent Faunal similarity curve based on the analyzed data and global oxygen-isotopic curve of Cenozoic by Zachos et al. (2001). Positions of South Africa from Paleocene to Miocene are assumed from tectonic movements as no fossil data was available. Dotted lines between Pleistocene and Recent indicate a switch from fossil data to records of living specimens. ? represents uncertainty as to the exact position of the region either through a weak clustering, a disagreement between the PAE and Cluster analyses or (as for South Africa Cretaceous to Pliocene) a lack of fossil data. Vertical dashed line for South Africa relates to a lack of fossil record to connect those time periods.

SUPPLEMENTARY DATA: MATERIAL AND METHODS

Materials

We constructed, compiled and analyzed a spatial and temporal database of all recorded fossil and living marine bivalve genera from the study area. In total >41,000 records representing 908 genera from 38 localities/time periods were analyzed. A matrix Fossil data were obtained from SOMBASE-GSCM (the Cenozoic Marine Fauna Database, Griffiths et al. 2003), the Paleobiology Database (<http://paleodb.org>) and additional references lacking in both databases (eg. Griffin & Pastorino 2006, Aguirre et al. 2008, Quaglio et al. 2008, 2010, Whittle et al. 2011, 2012, Beu 2009, Beu & Raine 2009, Beu & Taviani 2013). Recent data were obtained from SCAR Mar-BIN (<http://www.scarmarbin.be/>), OBIS (www.iobis.org) and Spencer et al. (2011) from latitudes presently higher than 34oS.

Southern South America, East Antarctica West Antarctica, New Zealand, Australia and southern Africa were considered as separate regions. West Antarctica includes outcrops found in Antarctic Peninsula (King George, Seymour, James Ross and Vega islands). East Antarctica includes McMurdo drill holes and McMurdo Erratics in McMurdo Sound, and Marine Plain in Vestfold Hills. For these analyses we combined the East and West Antarctic regions to reduce the gaps in the fossil record. This was done following preliminary analysis that showed strong similarities between the two Antarctic regions through time. Because modern sampling sites are more numerous than the geological outcrops, we use modern only data from regions corresponding to fossil sites in order to minimize the sampling effect.

Methods

Cluster analysis

PRIMER v6 (Clarke and Gorley 2006) was used to perform the cluster analysis between regions and also to examine overall similarity per time period using SIMPER (Clarke 1993). The cluster analysis was performed using non-transformed presence only data with quantitative Bray Curtis Similarity (Bray and Curtis 1957).

Parsimony Analysis of Endemicity (PAE)

PAE was run using Winclada version 1.00.08 (Nixon 2002). An artificial outgroup with an all-0 score was added to the data matrix prior to analysis. Heuristic searches were performed in TNT version 1.1. (Goloboff et al. 2007). In this paleobiogeographic work, the area PAE cladograms were not generated by analyzing areas temporally – i.e. obtaining one comparing area-cladograms for each time-slice and then comparing the set of cladograms with the entire studied time-interval – as initially proposed (Rosen 1988, Rosen & Smith 1988, see also Nihei 2006). Instead, we rather included all time-slices of each region as different “atemporal areas”, so that the temporal relationship between the areas would be recovered as part of the parsimony analysis. The topology chosen is one of the five most parsimonious resulting trees which better reflects geological area relationships.

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