

Paleobiogeography of the Danian molluscan assemblages of Patagonia (Argentina)



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ABSTRACT

A detailed quantitative analysis of bivalves and gastropods reported from Danian marine rocks of Patagonia (Argentina) allowed the identification of three molluscan biogeographic units that, from north to south, are identified as the Rocaguelian, Salamanca, and Dorotean Bioprovincias. Molluscan assemblages comprise Cosmopolitan, Paleoaustral, Gulf Coastal Plain and Endemic genera, which collectively give this fauna a distinctive signature, preventing them to be considered as related to any other assemblages recorded in the high latitudes of the Southern Hemisphere. Results obtained through the present research support the idea that the Weddellian Province did not extend to Patagonia during Danian times, proving that the geographic isolation of this region during that interval was enough to allow the development of separate biogeographic units from other austral regions. Moreover, it is demonstrated that, although significant even in northern Patagonia, Paleoaustral taxa were not dominant elements of Danian faunas. Composition of the molluscan faunas reflects the presence of warm-temperate waters in the region, and records a latitudinal temperature trend with slightly higher values in northern Patagonia than in the south. In addition, a discussion of the age of the Paleocene faunas has been incorporated. The assemblages contained in the Dorotea formation (Austral Basin), Lefipán and Roca formations (Cañadón Asfalto Basin), and Salamanca formation (Cañadón Asfalto and Golfo San Jorge basins) have been placed in the early Danian, based on the correlation with the accurately dated molluscan faunas of the Roca formation exposed in the Neuquina–Colorado Basin, and that of the Sobral and López de Bertodano formations (Antarctica).

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1. Introduction

Since the middle part of the 19th century it was proposed that the distribution and composition of marine invertebrate fossils during the Mesozoic–Paleogene boundary of southern high latitudes suggested communications among austral continents and islands.

The widely distributed, earliest Danian molluscan fauna of Patagonia (Argentina), is one of the oldest Paleocene assemblages recorded in the Southern Hemisphere, and for this reason plays an important role in the understanding of paleobiogeographic relationships. These molluscs drew the attention of paleontologists from the moment they were discovered by Darwin (1846) and later described by von Ihering (1903, 1907), and notwithstanding that they were still poorly understood, were incorporated into paleobiogeographic analyses (e.g. Zinsmeister, 1979, 1982). Moreover, the lack of the recognition that was being compared to uncoeval assemblages of Maastrichtian, Paleocene, and even Neogene ages, led to paleobiogeographic misinterpretations. The Maastrichtian and Paleocene ages of assemblages in the high latitudes of Argentina

have been properly discriminated only in recent times, and mainly through microfaunal analyses that provided an accurate stratigraphic scheme, upon which paleobiogeographic studies can be successfully accomplished. In light of this more precise age assessment of Paleocene units, recent systematic contributions, the discovery of collections made by E. Feruglio and R. Wichmann (housed in the Museo Argentino de Ciencias Naturales B. Rivadavia), and the substantial new material collected in Patagonia by the authors of the present paper, a more complex paleobiogeographic pattern for the early Danian is proposed.

The goals of this paper are (1) to examine the overall composition of the Danian molluscan faunas of Patagonia as well as to explore their relationships; (2) to assess whether assemblages of the Patagonian region constitute one or more biogeographic units; (3) to check if there was a latitudinal temperature control on the composition of Danian assemblages; (4) to test the validity of a previous hypothesis that suggested a northward extension of the Weddellian Bioprovince into the Patagonian region during the Danian (Zinsmeister, 1979, 1982; Olivero et al., 1990; Griffin and Hünicken, 1994); (5) to demonstrate the participation and fate of the Paleoaustral elements since the Maastrichtian in different regions of Patagonia: a—were they replaced during the Danian in northern Patagonia by warm-water genera with Tethyan affinities as proposed by Casadío (1994, 1998), Casadío et al. (1999, 2005), and Aguirre-Urreta et al. (2008)?; b—does the assemblage from the Lefipán Formation show

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weak affinities with Paleoaustral genera as Medina and Olivero (1993) suggested?; and (6) to check if there is any faunal evidence that indicates probable geographic connections among Patagonian basins.

2. Previous work

Hooker (1847) was the first naturalist who suggested that Antarctica, circumpolar islands and Isla Grande de Tierra del Fuego would belong to “one great botanical region” (Hooker, *op. cit.*, p. 209), providing the pioneer idea of the development of a “land communication” that in the past, and not necessarily at the same time, would have joined these islands with Chile, New Zealand, and Antarctica (Hooker, 1853, 1860).

Once Sowerby (in Darwin, 1846) had described the first Tertiary Patagonian molluscs, and von Zittel (1864) had recognized them in the Tertiary of New Zealand, researchers started looking for faunal affinities among southern continents. In this sense, Hutton (1872), based on geological evidences and distribution of Recent terrestrial and marine animals, proposed the existence of an “old Antarctic continent” during the Cretaceous–Miocene interval, when South America, New Zealand, Australia and South Africa, were all connected to Antarctica (Hutton, *op. cit.*, p. 251).

von Ihering (1891), proposed that during Mesozoic times there were two continents forming part of South America: Archiguayana and Archiplata. The latter one comprised Chile, Argentina, Uruguay, and Southern Brazil, and extended to the south in a South Pacific Antarctic continent that comprised Australia, New Zealand, New Guinea and the Polynesian Islands.

In the 20th century, many paleontologists mentioned similarities between Argentinean, Antarctic, and New Zealand faunas during the Cretaceous–Miocene interval (Wilckens, 1911, 1922, 1924; Fleming, 1962), but only von Ihering (1907) dealt with specific relationships during Danian times. Based on the presence of the genera *Perissodonta* (= *Struthiolaria*), *Neilo* (= *Malletia*), and *Lahillia*, Ihering (*op. cit.*) was the first author to suggest the development of a common molluscan fauna by the beginning of Paleocene times in New Zealand, Chile, and Patagonia. Curiously, the genus *Lahillia* has not been yet found in Danian horizons of Patagonia, while it has been recorded in the Maastrichtian and Eocene–Miocene of the region. Based also on these taxa, Davies (1934) followed Ihering's proposal, and indicated close similarities between the assemblages from the Wangaloan formation (late Danian, New Zealand) and the Roca and Salamanca formations (early Danian, Patagonia). In contrast, Finlay and Marwick (1937) postulated affinities among Wangaloan assemblages and the Maastrichtian faunas of Patagonia (Río Chico Formation), Antarctica (Lopez de Bertodano Formation), and Chile (Quiriquina Formation).

The distribution of the genus *Struthioptera*, representatives of the Family Struthiolariidae, and the then poorly known Paleocene–Eocene Antarctic assemblages, allowed Zinsmeister (1979, 1982) to shape previous ideas, creating the shallow-water, cool-temperate marine Weddellian Province, a biogeographic unit that was subsequently widely accepted among paleontologists. This province would have extended from West Antarctica to New Zealand, the northeastern coast of Australia, and southern South America. It would have originated in the latest Cretaceous, lasting until the late Eocene in Antarctica and South America, and the late Paleocene–early Eocene in New Zealand and Australia. On the basis of an almost unknown Tertiary fauna of Isla Grande de Tierra del Fuego, described by Steimann and Wilckens (1908), and at present considered of Miocene age, Zinsmeister (*op. cit.*) extended the Late Cretaceous–Paleogene Weddellian Province into southern South America. However, Stilwell (1991, 1994, 1997) and Stilwell et al. (2004) restricted the existence of the Weddellian Province to the Campanian–Maastrichtian interval and proposed that by the Paleocene, the Antarctic Peninsula should be considered as a separate province or subprovince of the Weddellian unit.

South American paleontologists have also speculated on the global affinities of the Patagonian assemblages. von Ihering (1902, 1907)

proposed similarities between faunas contained in the Roca and Salamanca formations, and Medina and Olivero (1993) and Medina et al. (1990) between coeval molluscs of the Lefipán and Salamanca formations. Griffin and Hünicken (1994), based on the common presence of genera characteristics of the Weddellian Province, found close similarities among Maastrichtian–Paleocene faunas from Dorotea's area and the late Cretaceous–early Tertiary assemblages of New Zealand.

3. Geological setting

The Maastrichtian–Danian transgression in Patagonia was one of the most extensive flooding events that covered the region during Cenozoic times. The Danian sedimentary rocks stretched along more than 1300 km in Patagonia covering Maastrichtian marine strata, and fossiliferous deposits are recorded from north to south, in the Neuquina–Colorado, Cañadón Asfalto, Golfo San Jorge and Austral basins, where a rich and fairly diverse shelf molluscan fauna is recorded. A summary and discussion of paleontological and stratigraphic contributions dealing with the Paleocene rocks of Patagonia was provided by Camacho (1992).

There is still no agreement among geologists about the paleogeographic reconstruction of the Danian transgression. On the one hand, it was proposed that there was an almost continuous Maastrichtian–Danian sea that extended eastwards of the Andean Range, with all basins to the north of the Deseado Massif being interconnected (Zambrano, 1987; Pascual et al., 1996; Page et al., 1999; Ortiz-Jaureguizar and Cladera, 2006; Musso et al., 2012) (Fig. 1A). However, on the other hand, some authors considered the Maastrichtian transgression to be more extensive than the Danian one, and that during the late interval, there was no connection among basins (Camacho, 1967, 1992; Bertels, 1975, 1979, 1995; Malumián and Caramés, 1995; Malumián and Nañez, 2011) (Fig. 1B).

3.1. Neuquina–Colorado Basin

Danian sedimentary rocks are exposed in the Neuquina Embayment (Fig. 1B; areas 1–3; Fig. 2). On the easternmost margins they are identified as the Arroyo Barbudo formation (Lizuán and Sepúlveda, 1978) and the El Fuerte formation (Kaschieter, 1963) (Fig. 1B; areas 4 and 5, respectively). Both units are almost devoid of fossils and only one oyster taxon has been identified. In comparison, the sedimentary sequence exposed in the Neuquina Embayment is highly fossiliferous and has been described by Uliana and Dellapé (1981), Legarreta and Gulisano (1989), Legarreta et al. (1989) and Barrio (1990). These deposits have been extensively studied over the last decades since the recognition of the K/Pg boundary, which has been in turn analyzed in detail by Concheyro (1995, 2001), Concheyro and Villa (1996), Papu et al. (1999), Nañez and Concheyro (1997), and Concheyro et al. (2002), among others. Faunas examined herein come from the Danian exposures of the Roca formation (Weaver, 1927) and Jaguel formation (Bertels, 1969). Both units constitute the uppermost part of the Malargüe Group and are represented by an upward-shallowing carbonate sedimentary sequence deposited in outer to inner shelf environments to hypersaline lagoons (Uliana and Dellapé, 1981). Danian molluscs are highly diversified and abundant and they were studied initially by Burckhardt (1901), Oppenheim (in Böhm, 1903), and von Ihering (1902, 1903, 1904, 1907), who carried out the revision of material collected by A. Romero, S. Roth, and W. Schiller in the vicinity of General Roca. More recently, some isolated groups of bivalves, such as oysters, mytilids, pinnids, and pectinoideans, were described by Casadío (1998), Griffin et al. (2008), and del Río et al. (2007, 2008), and gastropods by del Río (2012).

3.2. Golfo San Jorge Basin

The molluscs considered in the present paper were obtained from the Salamanca formation (Lesta and Ferello, 1972) exposed along the Atlantic coast, between Puerto Visser and Bahía Malaspina, along the Río Chico,

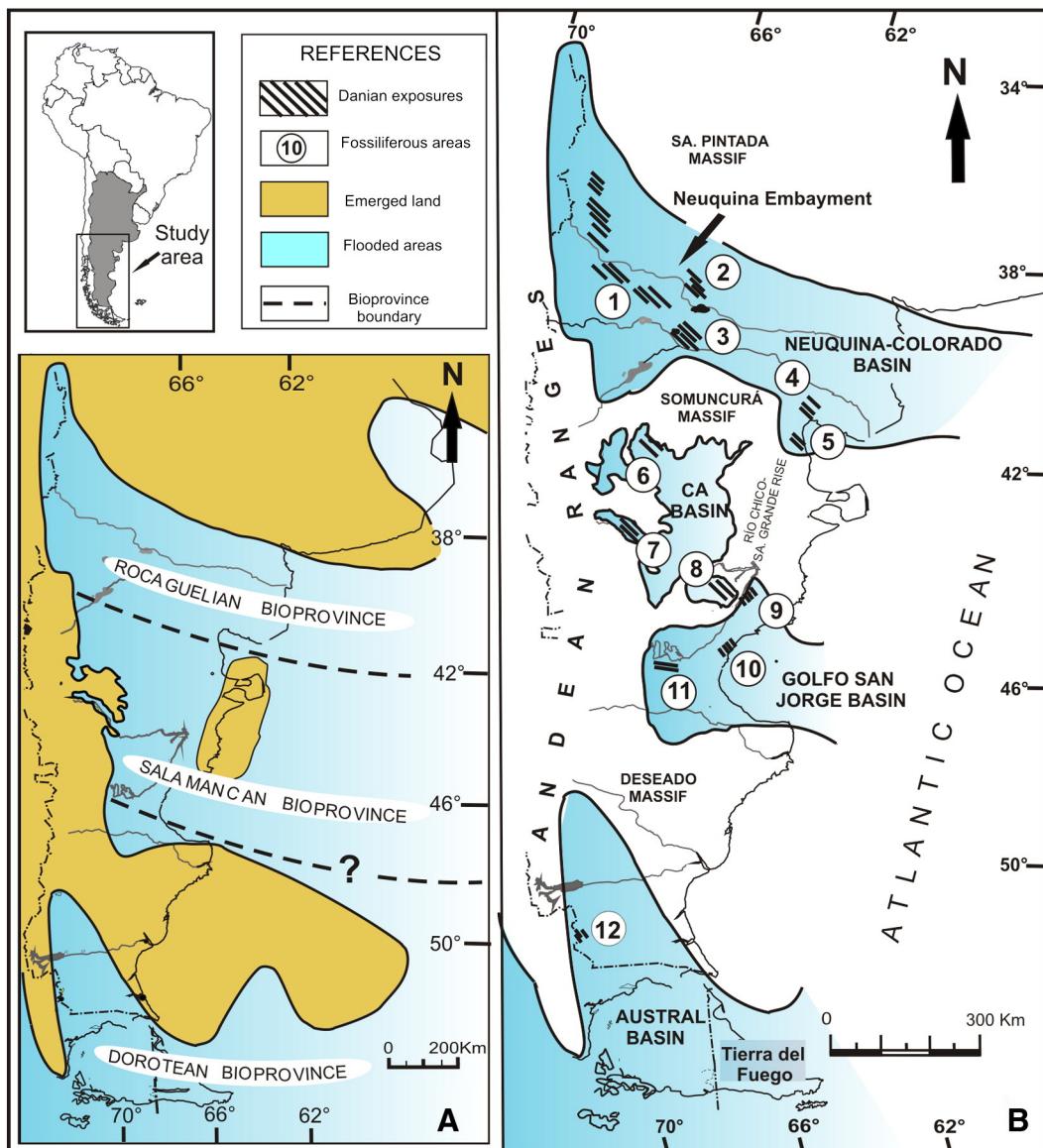


Fig. 1. A—Area covered by the Maastrichtian–Danian sea (modified from Musso et al., 2012). B—Paleogeographic location of Maastrichtian–Danian sedimentary basins (modified from Barcat et al., 1989; Cortiñas, 1996; Barrio, 1990). 1—Huantraico; 2—Southwestern La Pampa Province; 3—General Roca–Lago Pellegrini; 4—Bajo del Gualicho; 5—El Fuerte; 6—Ing. Jacobassi–Los Menucos; 7—Middle Valley Chubut River; 8—Sierra Cuadrada–Sierra de los Guanacos–Sierra de los Chacay; 9—Río Chico's area; 10—Puerto Visser; 11—Lake Colhue Huapi; 12—Río Turbio's area.

and to the south of the Colhue Huapi Lake (Fig. 1B, areas 9–11; Fig. 2). This unit consists of an intercalation of sandstones and siltstones deposited in a sublittoral marine environment of high energy (Masiuk, 1967; Andreis et al., 1975). Pioneer fossil collections were made by C. Ameghino in the area of the Río Chico, and the material was studied by von Ihering (1902). Subsequently, Feruglio (1936a,b) performed a global analysis of the Maastrichtian–Danian faunas describing the assemblage contained in the Salamanca formation exposed along the Atlantic coast, and from a new locality in Río Chico, 50 km south of C. Ameghino's site, a fauna later revised by Celeste (1949) and Masiuk (1967).

3.3. Cañadón Asfalto Basin

Molluscan assemblages considered herein were recorded in three areas situated on the margins of the basin: a) in the vicinity of the Sierra Cuadrada, Sierra de Los Guanacos, and Sierra de Los Chacays (Fig. 1B, area 8; Fig. 2), where molluscs occur in the Salamanca formation, and were initially described by Feruglio (1936a,b), using the material collected by J. Brandmayr. The Salamanca formation comprises an

intercalation of siltstones, sandstones, and coquinas with a fairly abundant, but poorly diversified fauna recorded in the Sierra de Los Guanacos, where most of the material comes from Chebli and Serraioto (1974) and Chebli et al. (1979); b) Ingeniero Jacobassi–Los Menucos region (Fig. 1B, area 6) where the Roca formation is exposed represented by a siliciclastic sequence deposited in an open, inner littoral or sublittoral environment dominated by fair weather and storm waves (Spalletti, 1988). These strata were discovered by Wichmann (1927), and further geological studies were carried out by Bertels (1969), Labudia and Bjerg (1994), and Getino (1995). Although the molluscs of the Roca formation are abundant and well-diversified, they have received scant attention. Few species were listed by Farinati et al. (1987) and Rodríguez et al. (1995), and a new gastropod assemblage was recently described by del Río (2012); c) Middle Chubut River Valley, between Piedra Clavada and Puesto Lefipán where the Lefipán formation (Lesta and Ferello, 1972) is exposed (Fig. 1B, area 7). It is represented by siliciclastic sediments deposited in a proximal, tide-dominated deltaic setting (Olivero and Medina, 1993; Scasso et al., 2012) and contains an abundant molluscan assemblage described by Feruglio (1936a,b) and Petersen (1946).

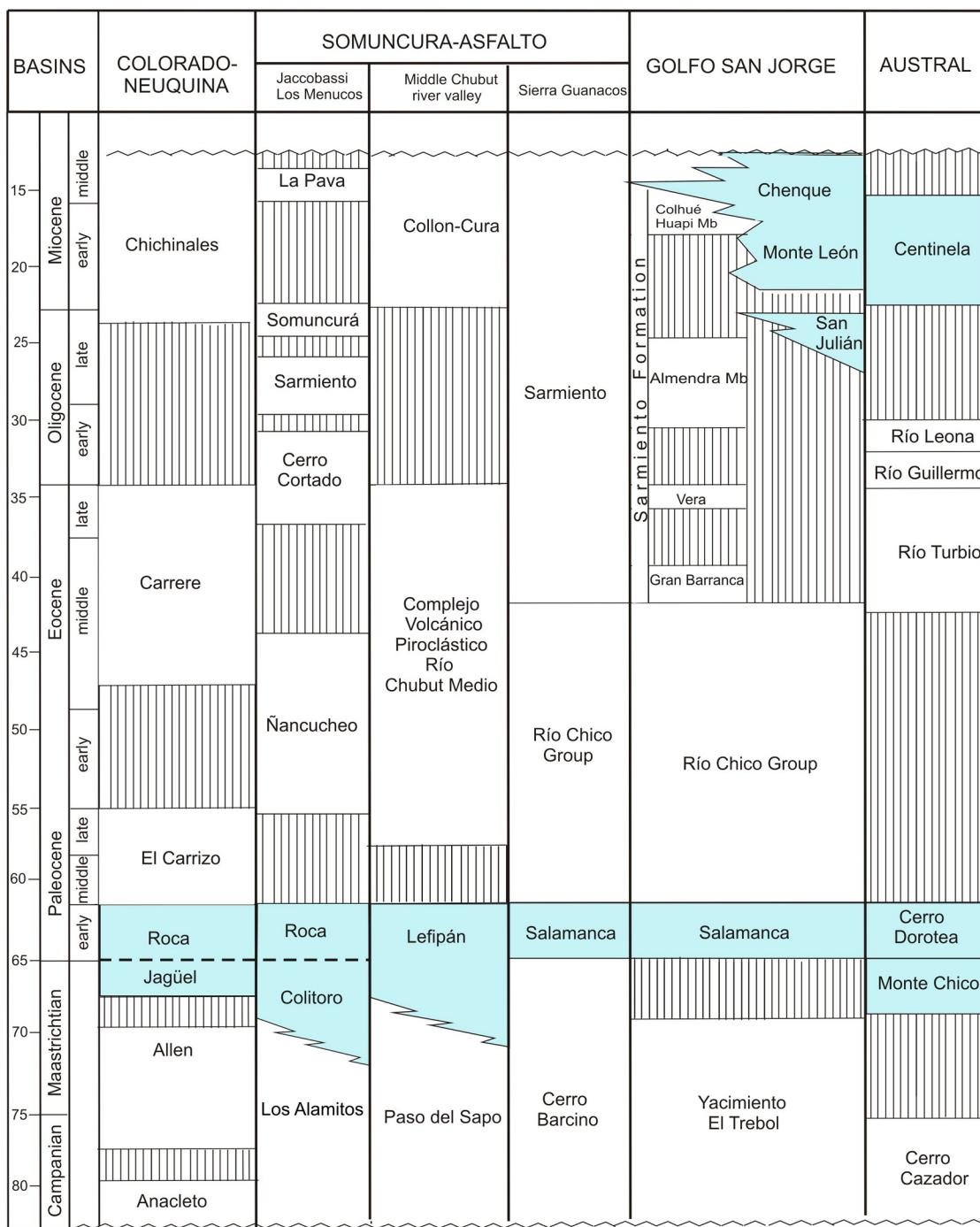


Fig. 2. Stratigraphy of Patagonian basins mentioned in the text. Marine formations in gray.

3.4. Austral Basin

Paleocene sedimentary rocks are recognized in the surroundings of Río Turbio and Isla Grande de Tierra del Fuego (Fig. 1B, area 12; Fig. 2). After pioneer geological studies made by Brandmayr (1945), Feruglio (1938, 1949), and Hünicken (1955) on the Maastrichtian-Paleocene sequence exposed in the area of Río Turbio, there were further detailed studies by Leanza (1972), Riccardi and Rolleri (1980), and Malumián and Panza (2000). Molluscs are reported from the Dorotea formation (Feruglio, 1938), exposed in the area located between the northern flank of the Cerro Dorotea and Estancia San Jorge. This unit overlies the late Maastrichtian-Danian horizons of the Monte Chico formation (Malumián and Panza, 2000) and is composed by a thick sedimentary sequence dominated by siliciclastic sandstones intercalated

with coquinas, and by conglomerates and coal beds. It represents a shallowing upwards event, from marine inner-shelf to continental environments (Malumián and Panza, *op. cit.*). The molluscan assemblage known from the Dorotea formation is one of the least diverse Patagonian Paleocene faunas, remaining unstudied until Camacho and Zinsmeister (1989), Griffin and Hünicken (1994), and Zinsmeister and Griffin (1995) revised the gastropod associations.

In Isla Grande de Tierra del Fuego, the only known Danian sedimentary rocks are devoid of molluscs and belong to the uppermost horizons of the Policarpo formation (Furque and y Camacho, 1949; Olivero et al., 2003). The late Paleocene Cabo Leticia and Punta Noguera formations yield unidentified shell fragments and oysters (Olivero et al., 2002) and the supposedly Paleocene assemblage described by Camacho (1957) and Buatois and Camacho (1993), from the Río Claro formation,

actually belongs in the Leticia formation of middle Eocene age (Malumián and Olivero, 2005).

3.5. Age of Paleocene molluscan assemblages

Based upon their foraminifera, calcareous nannofossil and palynomorph contents, the post-Cretaceous horizons of the Jagüel and Roca formations (Neuquina–Colorado Basin) were assigned to the earliest Danian (Casadío and Concheyro, 1992; Concheyro and Nañez, 1994; Concheyro and Villa, 1996; Nañez and Concheyro, 1997; Papu et al., 1999; del Río et al., 2007). The age of the highly fossiliferous horizons of the Roca formation in its type area has been recently analyzed, and the presence of three molluscan assemblages associated to the early Danian nannofossil zones NP1–NP2, NP3 and NP4 respectively, were recognized by del Río et al. (2011). In contrast to the accurate assignment of the Roca and Jaguel formations of the Neuquina–Colorado Basin, the age of marine units within the Austral, Golfo San Jorge, and Cañadón Asfalto basins deserves further discussion.

In the case of the Salamanca formation (Golfo San Jorge Basin), the foraminiferal content supports either an undifferentiated Danian age (Méndez, 1966; Masiuk, 1967) or restricts the unit to the late Danian (Bertels, 1975). The forams contained in the Roca formation exposed in the area of I. Jacobassi–Los Menudos (Cañadón Asfalto Basin) places the unit in the Danian s.l. (Náñez, 1998; Cuchi et al., 2001), while the ostracod assemblage confines it to the early Danian (Echevarría, 1995). The Dorotea formation (Austral Basin), is variously dated by forams as either in the late Paleocene (Caramés, 1996; Malumián and Caramés, 2002), at the base of the Paleocene, possible extending into the middle Paleocene (Malumián and Náñez, 2011, see Fig. 13), or Danian (Malumián et al., 2013). In addition, palynological study recently conducted by Povilauskas (2010), indicates a Danian age for this unit.

With reference to the Lefipán formation (Cañadón Asfalto Basin), Camacho (1967) demonstrated the existence of two assemblages of different ages, placing the oldest one in the Maastrichtian, but he did not make reference to the age of the younger one. Medina et al. (1990) recognized two other younger assemblages in the upper part of the unit of earliest and early Paleocene ages, respectively. Later, Medina and Olivero (1993) distinguished only one post-Cretaceous assemblage suggesting the lowest Paleocene age. The Lefipán formation is generally regarded as Maastrichtian–Paleocene because it overlies the Campanian–Maastrichtian Paso del Sapo Formation (Papú et al., 1988) and is overlain by ignimbrites that are correlated with part of the “Complejo volcánico piroclástico”, a complex of late Paleocene–middle Eocene age according to radiometric dating (Mazzoni et al., 1991; Aragón et al., 2010). According to this information, the upper part of the Lefipán Formation is perhaps best considered to be of undifferentiated Paleocene age.

Analysis presently fulfilled permits to contribute to the age assessment of these Patagonian assemblages. The record of genera and species in common among the Neuquina–Colorado, Golfo San Jorge and Cañadón Asfalto basins (Appendices 1 and 2), such as *Sacella tumida*, *Yoldia perdita*, *Talochlamys salamanca*, *Cubitostrea ameghinoi*, *Ostrea nequeana*, “*Phacoides*” *rocana*, *Venericardia australis*, “*Turritella*” *malaspina*, Aporrhaidae indet. (= *Rostellaria striatissima*), Aporrhaidae nov. gen., *Taioma* sp., *Microfulgur concheyroae*, and *Sulcobuccinum prominentum*, supports an early Danian age for all these faunas, based on correlation with the coeval, well documented and accurately dated assemblages of the Neuquina–Colorado Basin.

With the exception of *Perissodonta* and the new genus of Turritellidae, genera in common between the Austral (Dorotea formation) and Neuquina–Colorado basins are restricted to Maastrichtian survivors, and are not useful as chronostratigraphic tools. In turn, species in common with the San Jorge and Cañadón Asfalto basins (Appendix 1) (*Leionucula suboblonga*, *Neilo* cf. *N. gracilis*, ?*Astarte venatorum*, *Panopea thomasi*, *Panopea* sp., “*Turritella*” *ameghinoi*, *Crenilabium* (*Eoacteon*), *Fyfea beui*), as well as the closely similar congeneric species of *Heteroterma*, *Austrophaera*, *Pseudomaura*, ?*Zemacies*, *Priscaphander*,

and “*Tornatellaea*”, indicate strong affinities among all these basins. These faunal similarities are also observed between assemblages of the Austral Basin and the earliest Danian molluscs of Antarctica, which is indicated by the strongly similar congeneric species of *Neilo*, *Cucullaea*, *Panopea*, *Perissodonta*, *Austrophaera*, “*Pseudofax*”, *Taioma* and *Heteroterma*. All of these faunal evidences support the contention that the fauna of the Dorotea formation is early Danian in age.

4. Paleobiogeographic analysis

4.1. Material and methods

The present study incorporates 114 species and 86 genera of bivalves and gastropods contained in the Neuquina–Colorado Basin (NCB), Golfo San Jorge Basin (GSJB), Cañadón Asfalto Basin (CAB) and Austral Basin (AB) (Appendices 1 and 2). The basin was taken as an operational unit for the biogeographic analysis, because their borders acted as natural geographical limits during depositional times. The analysis comprises new collections made by the authors of the present paper and updated identifications of the material collected by R. Wichmann (CAB), A. Romero and S. Roth (NCB), C. Ameghino and V. Masiuk (SJB), and E. Feruglio, J. Brandmayr and A. Piatnizky (GSJB and CAB), previously studied by von Ihering (1902, 1907) and Feruglio (1936a,b). New material, and the Romero, Ameghino, Roth, Feruglio, and Wichmann collections are housed at the Museo de Ciencias Naturales B. Rivadavia (Buenos Aires) (MACN) and Masiuk's collection at the Facultad de Ciencias Exactas y Naturales (Universidad de Buenos Aires) (FCEyN).

Initially, the Patagonian assemblages were examined in order to establish discrete biogeographic units, an approach that was mainly based on the generic composition of faunas, since genera turned out to be the more useful and frequently used taxonomic level in paleobiogeographic studies (Campbell and Valentine, 1977; Shen and Shi, 2000; Martínez and del Río, 2002b). The selection of a biogeographical unit followed the same criterion applied by Martínez and del Río (2002a,b), who shaped bioprovinces on the basis of multivariate analyses and compared their values with those obtained by Campbell and Valentine (op. cit.). Subsequently, relationships existing among all Southern Hemisphere assemblages (Patagonia, Antarctica, Chatham Islands, Australia and New Zealand) were then established. To test and quantify these relationships, a dataset of the regional distribution of Paleocene genera was performed (Appendix 2). For New Zealand, Chatham Islands, and Australia, faunal lists were taken from Stilwell (2003) and Beu and Raine (2009), and for the Antarctica from material housed at the MACN and FCEyN, taking into account the revision carried out by Stilwell et al. (2004) and the comments made by Beu (2009), who modified the taxonomic assignment of almost the 50% of the Antarctic Danian species described by Stilwell et al. (op. cit.).

Similarity–dissimilarity in molluscan content among basins (presence–absence) was estimated using Jaccard and Simpson association coefficients and percentages of shared taxa. The Jaccard coefficient is computed as $M / (N_1 + N_2 - M)$, where M is the number of shared taxa in the samples; N_1 and N_2 are the taxa present in one sample and absent from the other. This coefficient has been widely used in both ecological and paleoecological studies because it provides a minimum distortion in binary data and does not take into account shared absence (Archer and Maples, 1987; Maples and Archer, 1988; Hammer and Harper, 2006). Although Simpson's is not a commonly used index today because of its limitations (e.g. it considers two samples identical if one is a subset of the other), it was included in the comparisons among bioprovinces with a view to comparing the results with those obtained by Campbell and Valentine (1977) and Martínez and del Río (2002b). The Simpson coefficient was calculated as M/N_{\min} , where M is the number of shared taxa and N_{\min} is the value of the smaller sample. To establish the relationships among basins, Q-mode (UPGMA) Cluster Analysis and non-metric multidimensional scaling (NMDS) were carried out. The computer program used was PAST v.3.01 (Hammer et al., 2001).

4.2. Results

4.2.1. Patagonian biogeographic units

The relationships among assemblages are displayed in the cluster and NMDS diagrams of Fig. 3 where it can be seen that basins cluster into three well defined groups: 1—Golfo San Jorge—Cañadón Asfalto basins (GSJB—CAB), 2—Neuquina—Colorado Basin (NCB), and 3—Austral Basin (AB). Both association coefficients (Simpson and Jaccard) and percentages of shared taxa obtained in the present paper (Tables 1 and 2) are similar to those values obtained by Campbell and Valentine (1977) on the Pacific Coast of the United States of America and by Martínez and del Río (2002b) when defining Miocene Bioprovinces in the Southwestern Atlantic Ocean. The development of three biogeographic units are recognized in Patagonia during Danian times, and from north to south, these are named as *Rocaguelian*, *Salamancan* and *Dorotean* Bioprovinces (Fig. 1A). As a whole, the fauna comprises Endemic (11.3%), Cosmopolitan (43.7%) and Paleoaustral (22.8%) taxa, and 18.3% of genera also recorded in the Paleogene Gulf Coastal Plain Province (GCP) of southern United States of America. Maastrichtian survivors comprise 33% of the fauna and these are also well represented both in the Maastrichtian of Chile and Antarctica. Table 3 shows taxonomic composition of the defined bioprovinces.

The *Rocaguelian Bioprovience* has 54 species and 49 genera, 12 of which are confined to this unit. It is identified by the abundance and diversity of oysters, small pectinids, carditids, nuculoids and turritellids. It is dominated by cosmopolitan taxa (57%), a few of them restricted to warm or warm-temperate waters (*Plicatula*, *Arca*, *Sulcobuccinum*, *Pycnodonte* (*Gryphaea*)), followed by 22% Paleoaustral elements (*Struthioptera*, *Pteromytea*, *Microfulgur*, *Cucullaea*, *Neilo*, *Taioma*, “*Tornatellaea*”, *Priscaphander*, and *Perissodonta*), most of them in common with remaining units, and some present in the area since the Cretaceous. This bioprovience records the occurrence of 12.2% GCP taxa (*Eburneopecten*, *Turkostrea*, *Venericardia*, and *Paranomia*) and also includes Endemic taxa (9.7%) such as *Rocalaria*, *Pseudotylostoma*, and new undescribed genera of Turritellidae and Aporrhaidae.

The *Salamancan Bioprovience* is distinguished by the presence of 85 species and 69 genera, and unlike the Rocaguelian Bioprovience, pectinids and oysters, although locally abundant, are not usually diverse. Twenty four genera are limited to this unit, among which are the GCP elements such as *Crenilabrum* (*Eoacteon*), *Claibornicardia*, *Bathytormus*, *Tejonia*, *Rotundicardia*, *Claibornicardia*, *Cidarina*, and *Cavoscalia* which constitute the 18.8% of total taxa. The Salamancan Bioprovience registers the southernmost extension in Patagonia of the cosmopolitan warm or warm-temperate *Arca*, *Barbatia*, and *Sulcobuccinum*, and the northernmost latitudinal extension of the Paleoaustral (25.45%) *Fyfea*, *Darwinices*,

Table 1

Distance matrices of the Danian genera of Argentina. A. Jaccard coefficient. B. Simpson coefficient.

A	C. Asfalto	G. San Jorge	Neuq.—Color.	Austral
C. Asfalto	1	0.447761	0.391892	0.21875
G. San Jorge	0.447761	1	0.353846	0.211538
Neuq.—Color.	0.391892	0.353846	1	0.15
Austral	0.21875	0.211538	0.15	1

B	C. Asfalto	G. San Jorge	Neuq.—Color.	Austral
C. Asfalto	1	0.731707	0.617021	0.636364
G. San Jorge	0.731707	1	0.560976	0.5
Neuq.—Color.	0.617021	0.560976	1	0.409091
Austral	0.636364	0.5	0.409091	1

Pseudomaura, *Spineilo*, ?*Zemacies*, *Marwickia*, and ?*Astarte*. Endemic genera constitute the 12.7% and, apart from those shared with the Rocaguelian unit, the Salamancan Bioprovience also includes *Pseudotylostoma*, *Austrophaera*, and a new buccinid genus (Buccinidae nov. gen. D, Table 3), which extends southwards to the Antarctic region (=“*Colus*” *delrioae* Stilwell et al., 2004).

The Dorotean Bioprovience has the lowest diversity of all units, containing only 23 species and 23 genera, with four restricted taxa: *Austroaporrhais*, *Scaphander*, “*Pseudofax*”, and ?*Spirogalerus*. Paleoaustral elements comprise 60.9% of the assemblage (?*Zemacies*, *Perissodonta*, *Darwinices*, *Pseudomaura*, *Fyfea*, *Microfulgur*, *Neilo*, ?*Astarte*, *Cucullaea*, *Taioma*, and *Priscaphander*). *Pseudotylostoma*, *Austroaporrhais*, and *Austrophaera* are the only endemic taxa (17.4%).

4.3. Comparison among Paleocene faunas of the Southern Hemisphere

When contrasting Patagonian assemblages with other faunas from the Southern Hemisphere it must be recognized that all these assemblages are not necessarily contemporaneous as they comprise: (a) early or earliest Danian faunas (Roca, Jagüel, Salamanca, Dorotea, Lefipán formations [Patagonia] and López de Bertodano and Sobral formations [Antarctica]); (b) late Danian assemblages: Wangaloan formation [New Zealand (1)] and Chatham Islands; and (c) Selanian–Thanethian faunas from New Zealand (2) and Australia. Fig. 4 and Table 4 show that, on the one hand, clustering of Patagonian basins remains the same as when analyzed separately and, on the other, the Austral Basin clusters together with the Antarctica fauna with a very low Jaccard coefficient of 0.25. Like the fauna of the Austral Basin, the Antarctic one is poorly diversified and is constituted by 36 genera, does not have shared species with the Patagonian region, and only 15.3%

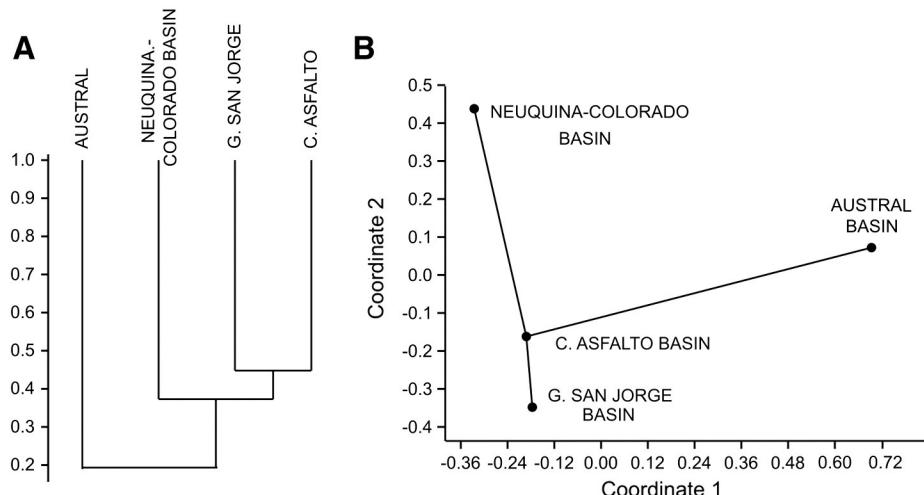


Fig. 3. Relationships among the Danian genera of Argentina. A. Cluster analysis. Jaccard coefficient, ccc: 0.9741. B. Non metric multidimensional scaling. Jaccard coefficient. Stress: 0.

Table 2

Percentages of shared genera among the Paleocene faunas of Southern Hemisphere.

	Patagonian Basins				Antarctica	Chatham Is.	N. Zealand (1)	N. Zealand (2)	Australia
	C. Asfalto	G. San Jorge	Neuq.–Color.	Austral					
C. Asfalto	100								
San Jorge	30.93	100							
Neuq.–Color.	28.15	26.14	100						
Austral	17.95	17.46	13.04	100					
Antartica	12.9	7.69	8.23	15.25	100				
Chatham Is.	0	4.85	2.73	1.19	2.06	100			
N. Zealand (1)	8.18	5.55	5.96	9.6	10.14	6.75	100		
N. Zealand (2)	1.47	0	3.33	5.88	4.25	0	5.31	100	
Australia	8.51	7.94	8.27	5.61	9.17	4.83	12.9	4.21	100

comprise genera common to both regions, among which there are the endemic genera *Pseudotylostoma* and *Austrophaera*, and the Paleoaustral elements *Perissodata*, *Taioma*, *Neilo* and *?Astarte* (Table 2). These data prevents us from considering the Antarctic faunas as belonging to the Dorotean Bioprovince or to any other Patagonian biogeographic units herein defined, as formerly proposed by Stilwell et al. (2004), who anticipated that the Antarctic assemblage belongs to a distinctive bioprovince.

In turn, the Patagonian and Antarctica faunas cluster with the assemblages of New Zealand (1), and Australia and, at a second level with New Zealand (2) and Chatham Islands, albeit with an even lower Jaccard coefficient value than that existing between Patagonia and Antarctica (Table 4). Except for some shared taxa, such as the long-ranging cosmopolitan *Leionucula*, *Nucula*, and *Panopea*, and the Paleoaustral *Priscaphander*, *Neilo*, *Fyfea*, *Pseudamaura*, *Microfulgur*, *?Zemacies*, *Darwinices*, *Spineilo*, *Marwickia*, *?Spirogalerus*, and *Taioma*, assemblages of New Zealand, Chatham Islands and Australia are highly endemic. Moreover, the endemism of the Patagonian molluscs (*Austrophaera*, *Rocalaria*, *Struthiochenopus*, *Pseudotylostoma*, *Astroaporrhais*, *Aporrhaidae* nov. gen. and *Turritellidae* nov. gen.), the arrival of Gulf Coastal Plain taxa (*Cavoscala*, *Claibornicardia*, *Rotundicardia*, *Bathytormus*, *Cavoscala*, *Cidarina*, *Eburneopecten*, “*Euvola*”, *Crenilabium* (*Eoacteon*), *Tejonia*), and the absence of the typical Indo-Pacific warm-water genera, characteristic of New Zealand and Australian faunas, clearly indicate that the isolation of all these regions during the Paleocene led to the development of separate biogeographic units. These results confirm that the Weddellian Province did not extend into Patagonian regions during Danian times as previously supposed (Zinsmeister, 1979, 1982; Griffin and Hünicken, 1994).

5. Discussion

The term “Paleoaustral” elements was coined by Fleming (1962) who defined them as austral elements, “consisting of plants and animals more distantly related to those of other southern lands, some with a fossil record going back to the Tertiary or Mesozoic times, which are no longer being dispersed and which have such poor dispersal abilities that many biologists have considered they were distributed along land connections linking southern lands with Antarctica” (Fleming, 1962, p. 97). Zinsmeister (1982) provided a list of Paleoaustral genera represented in the Wangaloan and Boulder Hill faunas (New Zealand) and stated that they were also well represented in Antarctica and southern South America, where they would exceed 50% during the Late Cretaceous–Early Tertiary interval. Thus, these elements came to be considered characteristic of the Weddellian Province, and were indistinctively referred to as Paleoaustral or Weddellian. Subsequently, Griffin and Hünicken (1994) enlarged their number with the inclusion of the Maastrichtian–Danian taxa of the Río Turbio region (see Stilwell et al., 2004, for further discussion of identity of Paleoaustral elements).

Whether or not Paleoaustral elements became extinct in Patagonia after the Weddellian Province had lost its identity, the number of survivor genera and their northernmost distribution in the region, has been a matter of discussion. Camacho (1992) stated that the Maastrichtian fauna from the Neuquina–Colorado Basin exhibits strong affinities with the

“austral one” (Paleoaustral), but that during the Danian, faunas showed a resemblance with those of the GCP. Casadio (1994) and Feldmann et al. (1995) proposed that the Danian assemblages with Weddellian affinities of the Neuquina–Colorado Basin, had been replaced by warm-water Tethyan genera. Casadio (1998), Casadio et al. (1999, 2004, 2005) and Aguirre-Urreta et al. (2008) confirmed the presence of Paleoaustral elements in the Neuquina Basin during the Maastrichtian but “starting in the Late Maastrichtian (late Chron 30N–Chron 29R), and specially from the Danian onwards, the Weddellian fauna was replaced in Northern Patagonia by warm-taxa much akin to coeval faunas with Tethyan affinities.” (Casadio et al., 2005, p. 508). However, del Río et al. (2008) demonstrated that Paleoaustral taxa largely survived in northern Patagonia well into Danian, and the present study confirms that they were not replaced during this interval in the Neuquina–Colorado Basin, and were also abundant in the Golfo San Jorge and Cañadón Asfalto basins. Paleoaustral genera remained in the area during the Maastrichtian–Danian interval, when they were widely distributed from Antarctica to northern Patagonia (Table 5), even after the Weddellian Province lost its identity at the end of the Maastrichtian. The Rocaguelian Bioprovince records the northernmost geographic extension of *Fyfea* and *Taioma*, two genera that were also thought to be restricted to the Maastrichtian. It must be pointed out that Beu (2009) placed *Clinura* sp. of Kollmann and Peel (1983), from the Danian of West Greenland, in *Taioma*, but this is a doubtful assignment that deserves further discussion. These results clearly indicate that the Paleoaustral taxa were common components of the Danian Patagonian assemblages. Even so, these faunas cannot be considered as being dominated by those elements, because the occurrence of endemic and GCP genera print a distinctive feature on the assemblages. The significant proportion of all these components indicates that Patagonian faunas had a more complex origin than just being the sole result of persistent austral genera that were present in the area since the Maastrichtian times.

The hypothesis of an almost continuous Maastrichtian–Danian sea (Pascual et al., 1996; Page et al., 1999; Ortiz-Jaureguizar and Cladera, 2006; Musso et al., 2012) assumes overflooding of structural highs (i.e. Deseado and Somuncurá Massifs, Fig. 1B). To date, only some temporarily and geographically restricted connections have been demonstrated by Lesta and Ferello (1972), Cortiñas (1996), Page et al. (op. cit.), and Scasso et al. (2012). Findings discussed in the present paper contribute to this issue. Similarity coefficients and percentages of shared taxa (Tables 1 and 2) indicate that, at least during isolated intervals, those Patagonian basins lying to the north of the Deseado Massif could have been connected, thus facilitating faunal interchanges. Moreover, species in common among basins (23.4% between CA and N; 22.1% between CA and GSJ; 14% between GSJ and NC) also reinforce this idea. However, faunas of the Austral Basin does not bear any resemblance with assemblages of remaining basins (Tables 1 and 2; Fig. 4), and geographic connections, if any, with other regions of Patagonia, cannot be demonstrated at this time based upon molluscan similarities.

Paleotemperature values from the Danian seas of Patagonia also have been a controversial matter. Based on foram assemblages, Bertels (1970) claimed the development of warm-temperate conditions, and Leanza

Table 3

Geographic distribution of genera in the Danian bioprovinces as presently defined herein.

Bioprovinces	Dorotean	Salamancan		Rocaguelian
Basins	Austral	Golfo san Jorge	Cañodón Asfalto	Neuquina-Colorado
<i>Acesta</i> *				
<i>Perissodonta</i>				
<i>Pseudotylostoma</i> *				
<i>Leionucula</i> *				
<i>Taioma</i> *				
<i>Neilo</i> *				
" <i>Tornatellaea</i> "				
<i>Priscaphander</i> *				
<i>Turritellidae</i> nov. gen				
<i>Heteroterma</i> *				
? <i>Astarte</i> *				
<i>Panopea</i> *				
<i>Austrophaera</i> *				
<i>Crenilabiun</i> (<i>Eoacteon</i>)*				
<i>Pseudomaura</i>				
<i>Darwinices</i> *				
<i>Fyfea</i> *				
? <i>Zemacies</i>				
" <i>Pseudofax</i> "				
<i>Spirogalerus</i>				
<i>Astroaporrhais</i> *				
<i>Scaphander</i>				
<i>Euvola</i>				
<i>Barbatia</i>				
<i>Cancellariidae</i> indet.				
<i>Caryocorbula</i>				
<i>Buccinidae</i> gen B				
? <i>Larma</i>				
<i>Ledina</i> *				
<i>Claibornicardia</i>				
<i>Buccinidae</i> gen C				
<i>Buccinidae</i> gen A				
<i>Nucula</i>				
<i>Volutidae</i> indet.				
<i>Buccinidae</i> nov.gen D				
<i>Tejonia</i>				
<i>Arca</i>				
<i>Glycymerita</i> *				
<i>Sacella</i>				
<i>Aporrhaidae</i> indet.				
<i>Gregariella</i>				
<i>Aporrhaidae</i> nov.gen.				
<i>Phacoides</i>				

Bioprovinces	Dorotean	Salamancan		Rocaguelian
Basins	Austral	Golfo san Jorge	Cañodón Asfalto	Neuquina-Colorado
<i>Cubitostrea</i> *				
<i>Gyrosscala</i>				
<i>Sulcobuccinum</i>				
<i>Venericardia</i>				
<i>Microfulgur</i>				
<i>Yoldia</i> *				
<i>Gryphaostrea</i> *				
<i>Talochlamys</i>				
<i>Pycnodonte</i> (<i>Gryphaea</i>)*				
<i>Calyptraeidae</i> indet.				
<i>Marwickia</i>				
<i>Spineilo</i>				
<i>Bathyformus</i>				
<i>Acispa</i>				
<i>Rotundocardia</i>				
<i>Cidarina</i>				
<i>Harpidae</i> nov. gen				
<i>Ringiculidae</i> indet.				
<i>Cardites</i>				
<i>Cavoscala</i>				
<i>Cucullaea</i> *				
<i>Pinna</i> *				
<i>Rocalaria</i>				
? <i>Dosinia</i>				
<i>Fusinus</i> *				
<i>Globisininae</i> indet.				
<i>Lucinidae</i> gen. A				
<i>Patellogastropoda</i> indet.				
<i>Priscophicus</i>				
<i>Pteromyretea</i>				
<i>Struthioptera</i> *				
<i>Paronomia</i> *				
<i>Limea</i> (<i>Pseudolimea</i>)*				
<i>Turkostrea</i> *				
? <i>Atrina</i> *				
<i>Parvamussium</i>				
<i>Plicatula</i> *				
<i>Delectopecten</i>				
<i>Eburneopecten</i>				
<i>Nuculana</i>				
<i>Nemodon</i>				
<i>Lucinidae</i> sp. B				
" <i>Utraria</i> "				

* Maastrichtian survivors into Danian times.

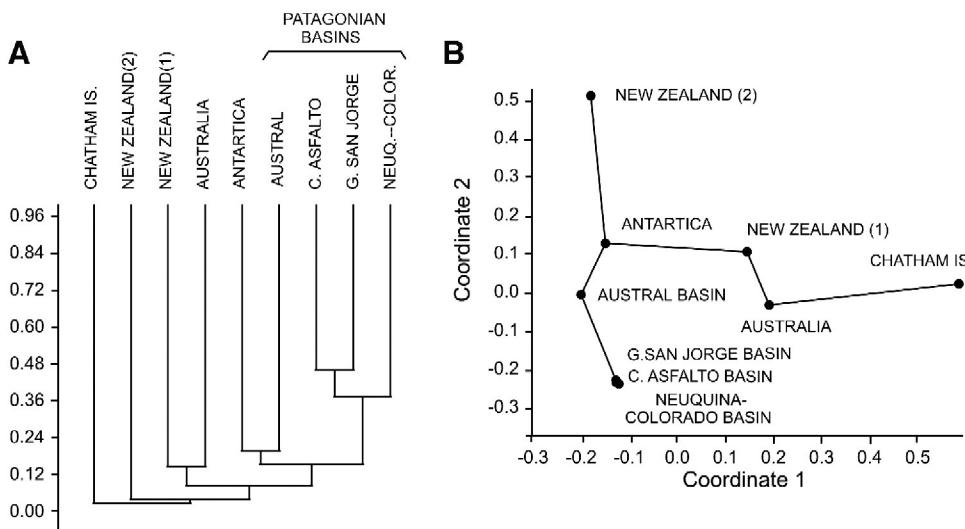


Fig. 4. Relationships among the Paleocene genera of the Southern Hemisphere. A. Jaccard coefficient, ccc: 0.9628. B. Non metric multidimensional scaling. Jaccard coefficient. Stress: 0.124.

and Hugo (1985) proposed the presence of warm waters. Later, Feldmann et al. (1995), based on Danian brachyurans, inferred tropical to warm-temperate settings, with congeneric species from the Northern Atlantic and Tethyan regions. But this conclusion must be evaluated in the light of subsequent revisions of decapods (Feldmann and Schweitzer, 2006, and bibliography herein), that modified the systematic status of most of the Danian decapod faunas previously described, some of which became endemic genera that, according to Feldmann and Schweitzer (*op. cit.*), should be considered inhabitants of temperate waters. Casadío (1998), Casadío et al. (1999, 2004), and Parma and Casadío (2005) all proposed the occurrence in northern Patagonia of a warm water fauna (corals, echinoids and molluscs) with Tethyan affinities during the Danian. However, regarding the echinoids (del Río et al., 2007; Martínez et al., 2011), with the exception of *Micropsis*, which is known since the Danian, genera are recorded since the Late Cretaceous in the Tethyan and Boreal realms as well (*Gauthiera*, *Gomphechinus*). Others, like *Bolbaster*, *Diplodetus*, *Hemister*, and *Linthia*, have a cosmopolitan distribution including Australia, New Zealand, India and Madagascar of the South Temperate Realm. In reference to species composition, a high degree of endemism is observed, that probably will be

increased through future taxonomic revisions. Therefore, the echinoid faunas cannot be considered as restricted to warm waters. In addition, nautilids described by Casadío et al. (1999) (*Eutrephoceras*, *Cimomia*, *Hercoglossa*) are also cosmopolitan genera distributed in both tropical and subtropical regions during the Maastrichtian–Paleogene interval (Kummel, 1956; Halder, 2012), even in the Eocene cool temperate waters of the Antarctic Peninsula (Ivany et al., 2008), where *Cimomia* has been recorded in the La Meseta Formation (Dzik and Gazdzicki, 2001). Another example of these eurythermal genera is the finding of *Eutrephoceras* in the Maastrichtian–Danian cool-temperate Austral Realm (Stilwell and Zinsmeister, 1987a,b; Stilwell and Grebneff, 1996).

The composition of Danian molluscs of Patagonia reveals the existence of warm-temperate waters in the region. This conclusion is supported by the occurrence of Paleoaustral elements and GCP taxa. The former genera are warm temperate taxa (Beu, 1966; see Stilwell, 2003 and discussion herein), and do not embrace assemblages of cool-temperate aspects such as considered by Zinsmeister (1982), Griffin and Hünicken (1994) and Maxwell (2000). Furthermore, the GCP taxa are recorded in the warm temperate subtropical region of the Gulf Coastal Plain in the southeastern United States (Siesser, 1984).

Table 4

Distance matrices of the Paleocene genera of Southern Hemisphere. A. Jaccard coefficient. B. Simpson coefficient.

A	Patagonian basins				Antarctica	Chatham Is.	N. Zealand (1)	N. Zealand (2)	Australia
	C. Asfalto	G. San Jorge	Neuq.–Col.	Austral					
C. Asfalto	1	0.462687	0.378378	0.238095	0.188406	0	0.121429	0	0.112
G. San Jorge	0.462687	1	0.353846	0.230769	0.152542	0.032967	0.0916031	0	0.0964912
Neuq.–Col.	0.378378	0.353846	1	0.152542	0.16129	0.0208333	0.0970149	0	0.121739
Austral	0.238095	0.230769	0.152542	1	0.25	0	0.106195	0	0.0808081
Antarctica	0.188406	0.152542	0.16129	0.25	1	0.0126582	0.131579	0.0285714	0.090099
Chatham Is.	0	0.032967	0.0208333	0	0.0126582	1	0.0472973	0	0.0378788
N. Zealand (1)	0.121429	0.0916031	0.0970149	0.106195	0.131579	0.0472973	1	0.0471698	0.177215
N. Zealand (2)	0	0	0	0	0.0285714	0	0.0471698	1	0.021978
Australia	0.112	0.0964912	0.121739	0.0808081	0.0990099	0.0378788	0.177215	0.021978	1

B	Patagonian basins				Antarctica	Chatham Is.	N. Zealand (1)	N. Zealand (2)	Australia
	C. Asfalto	G. San Jorge	Neuq.–Col.	Austral					
C. Asfalto	1	0.738095	0.608696	0.652174	0.481481	0	0.309091	0	0.254545
G. San Jorge	0.738095	1	0.547619	0.521739	0.333333	0.0731707	0.292683	0	0.268293
Neuq.–Col.	0.608696	0.547619	1	0.391304	0.37037	0.0444444	0.288889	0	0.311111
Austral	0.652174	0.521739	0.391304	1	0.434783	0	0.521739	0	0.347826
Antarctica	0.481481	0.333333	0.37037	0.434783	1	0.037037	0.555556	0.111111	0.37037
Chatham Is.	0	0.0731707	0.0444444	0	0.037037	1	0.132075	0	0.0943396
N. Zealand (1)	0.309091	0.292683	0.288889	0.521739	0.555556	0.132075	1	0.555556	0.333333
N. Zealand (2)	0	0	0	0	0.111111	0	0.555556	1	0.222222
Australia	0.254545	0.268293	0.311111	0.347826	0.37037	0.0943396	0.333333	0.222222	1

Table 5

Geographic distribution of Maastrichtian taxa survivors into Danian times. Antarctica (Lopez de Bertodano Formation); Chile (Quiriquina Formation); Neuquina–Colorado Basin (Jagüel Formation); Cañadón Asfalto Basin (Lefipán Formation); Austral Basin (Monte Chico Formation).

Compiled from Petersen (1946), Camacho (1968), Stinesbeck (1986), Zinsmeister and Macellari (1988), Olivero et al. (1990), Griffin and Hünicken (1994), Casadio (1998), Bandel and Stinesbeck (2000), Stilwell et al. (2004), Griffin et al. (2005), and Casadio et al. (2005).

Genera	Antartica	Chile	Austral Basin	C. Asfalto Basin	Neuquina–Colorado Basin
<i>Leionucula</i>	X	X	X	X	
<i>Ledina</i>				X	
<i>Yoldia</i>		X			
<i>Neilo</i> *	X	X	X	X	X
<i>Cucullaea</i> *	X		X	X	
<i>Glycymeris</i>				X	X
<i>Pinna</i>	X		X	X	
<i>Atrina</i>					X
<i>Plicatula</i>					X
<i>Paranomia</i>				X	X
<i>Limea (Pseudolimea)</i>				X	X
<i>Pycnodonte (Gryphaea)</i>	X			X	X
<i>Cubitostrea</i>					X
<i>Gryphaostrea</i>					X
<i>Turkostrea</i>					X
<i>Acesta</i>	X				X
<i>Astarte</i> *			X	X	
<i>Panopea</i>	X	X		X	X
<i>Struthioptera</i> *				X	X
<i>Austroaporrhais</i>	X	X	X	X	
<i>Pseudotylostoma</i>			X		
<i>Darwinices</i> *		?	X		
<i>Austrophera</i>		X	X		
<i>Heteroterma</i>			X		
<i>Fyfea</i> *			X		X
<i>Taioma</i> *	X		X	X	
<i>Crenilabium (Eoacteon)</i>		X		X	
<i>Priscaphander</i> *			X	X	

* Paleoastral elements.

When discriminating the composition of assemblages of the Rocaguelian, Salamanca, and Dorotean Bioprovinces, a slight northwards decrease in percentages of Paleoastral taxa can be assessed and an increase in GCP elements, along with the occurrence of warm water cosmopolitan genera that are confined to the basins placed to the north of the Deseado Massif can be observed. This compositional variation points to the development of an incipient latitudinal climatic trend, with a southward decrease in temperature, with warmer conditions in northern Patagonia than in the south, but within an overall warm temperate context. The results achieved support the placement of Patagonia in the warm-temperate belt during Danian times, as recently proposed by Iglesias et al. (2011) based on plants. The Dorotean Bioprovience should be considered as a transitional area placed between the warm-temperate waters to the north, and the cool-temperate ones of the Antarctic Peninsula (Kemp et al., 2014) to south.

This conclusion is rather different from that indicated by the distribution of the shelf cosmopolitan Midway-type benthonic foraminiferal faunas, which suggests “equitable climatic conditions (lower polar-equatorial thermal gradient) and warmer, more uniform thermal structure of the oceans” (Berggren and Aubert, 1975, p.73) for the Paleocene, an idea later corroborated by Malumián and Caramés (1995) and Malumián et al. (1998) for the Danian sea of Patagonia.

6. Conclusions

- Composition of molluscan faunas recorded in the Golfo San Jorge, Cañadón Asfalto, and Austral basins supports an early Danian age by correlation with the coeval, accurately dated assemblages of the Roca formation (Neuquina–Colorado Basin) and of the Sobral and Lopez de Bertodano Formations (Antarctica).
- Three paleobiogeographic units are identified, that from north to south are named: Rocaguelian, Salamanca, and Dorotean Bioprovinces. The development of these units in the southwestern Atlantic Ocean reinforces the assumption that the Weddellian Province did not extend into Patagonia in Danian times, a region that was geographically

isolated during that interval resulting in separated biogeographic units from the remaining austral continents.

- Quantitative analysis confirms that the early Danian Antarctic fauna constituted a separate bioprovience as formerly proposed by Stilwell et al. (2004).
- Danian assemblages of Patagonia comprise Paleoastral, Cosmopolitan, Endemic and Gulf Coastal Plain elements.
- Paleoastral taxa survived into Danian times even in northern Patagonia, where they represent 19% of the total fauna in the Rocaguelian Bioprovience and 25.5% in the Salamanca Bioprovience.
- Species and genera in common among basins strengthen the idea that during Danian times, the Neuquina–Colorado, Golfo San Jorge, and Cañadón Asfalto basins were interconnected.
- Occurrence of Paleoastral and Gulf Coastal Plain taxa support the presence of a warm-temperate sea in Patagonia during the Danian.
- Variation in the composition of the molluscs of the Rocaguelian to the Dorotean Bioprovinces records a latitudinal trend in climatic conditions, with slightly warmer temperatures in northern Patagonia than in the south, but always in a warm-temperate context.
- The Dorotean Bioprovience constitutes a transitional area between the Warm-Temperate Belt and the Cool-Temperate region of the Antarctic Peninsula during Danian times.

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Appendix 1. Distribution of the Danian gastropod and bivalve species in Patagonia described and/or illustrated in [1] von Ihering (1903); [2] von Ihering (1907); [3] Feruglio (1936a); [4] Feruglio (1936b); [5] Petersen (1946); [6] Masiuk (1967); [7] Medina et al. (1990); [8] Griffin and Hünicken (1994); [9] Rodríguez et al. (1995); [10] Casadío (1998); [11] Griffin et al. (2005); [12] del Río et al. (2007); [13] Griffin et al. (2008); [14] del Río et al. (2008); [15] del Río et al. (2011); [16] del Río (2012); [17] Griffin and Pastorino (2013); [18] Santelli and del Río (2014); [19] Zinsmeister and Griffin (1995); [20] Perez and del Río (2012); [21] Wilckens (1905). Whenever it was possible, references include illustrations of type material.

SPECIES	NEUQ.-COLOR BASIN	C. ASFALTO BASIN	G. SAN JORGE BASIN	AUSTRAL BASIN	REFERENCES
<i>Leionucula pervicax</i> (Feruglio, 1936b)	-	x	x	-	[4] Pl.23, figs. 4-5
<i>Leionucula frenguelli</i> (Feruglio, 1936b)	-	-	x	-	[4] Pl. 22, fig. 11
<i>Leionucula suboblonga</i> (Wilckens, 1905)	x	x	-	x	[15] Fig.11.17 (= <i>L. dynastes</i> Ihering, 1907)
<i>Nuculana</i> sp.	x	-	-	-	this paper
<i>Sacella tumida</i> (Feruglio, 1936b)	x	x	x	-	[4] Pl.23, figs.12-15
<i>Ledina lepida</i> (Feruglio, 1936b)	-	x	x	-	[4] Pl.23, figs.16-17
? <i>Nemodon</i> sp.	x	-	-	-	this paper
<i>Yoldia (Calohardia) perdita</i> (Feruglio, 1936b)	x	x	x	-	[4] Pl.23, figs.18-21 (= <i>Y. lanceolata</i> Fer. Pl.23, fig.22); [15] Fig.11.5-6
<i>Spineilo</i> sp.	x	x	-	-	[12] Fig.3.Q
<i>Neilo subornata</i> (Feruglio, 1936b)	x	x	-	-	[4] Pl. 23, figs. 25-26
<i>Neilo</i> sp.	x	-	-	-	[15] Fig.11. 4
<i>Neilo cf. N. gracilis</i> Wilckens, 1905	-	x	-	x	[21] Pl.5, fig.10 *
" <i>Malletia</i> " undulostriata (Feruglio, 1936b)	-	-	x	-	[4] Pl.23, figs. 23-24
" <i>Malletia</i> " descipiens (Feruglio, 1936b)	-	-	x	-	[4] Pl. 23, fig. 27
<i>Arca</i> n.sp.	-	-	x	-	this paper
<i>Arca ameghinorum</i> (Ihering, 1907)	x	-	-	-	[15] Fig.10.11-12
<i>Barbatia</i> n. sp.	-	-	x	-	this paper
<i>Cucullaea rocana</i> Ihering, 1903	x	x	-	-	[1] Pl. 2, fig. 7
<i>Cucullaea</i> cf. <i>C. Antarctica</i> Wilckens, 1905	-	-	-	x	[21] Pl.6, figs.5-6 *
<i>Glycymeris</i> sp.	x	x	-	-	this paper
<i>Glycymeris feruglio</i> Celeste, 1940	-	x	x	-	[5] Pl. 10, figs.1-2; [6] Pl. 5, fig.1; [9] PL. 2, fig. D
<i>Gregariella amara</i> Griffin et al., 2008	x	-	-	-	[13] Figs.3.5-8; [15] Fig.11.18
<i>Gregariella aprilis</i> (Feruglio 1936b)	-	-	x	-	[4] Pl.21, fig.7
<i>Pinna</i> sp.	x	x	-	-	[13] Fig.4.2
? <i>Atrina</i> sp.	-	-	-	-	[13] Fig.4.7
<i>Plicatula</i> sp.	x	-	-	-	[15] Fig.11.12
<i>Parvamussium bayosense</i> de Río et al. 2008	x	-	-	-	[14] Figs.3.1-3.5
<i>Talochlamys salamanca</i> (Ihering, 1903)	x	x	x	-	[15] Fig.11.16,19
<i>Delectopecten neuquensis</i> de Río et al.2008	x	-	-	-	[14] Figs.4.1-4.7
<i>Eburneopecten</i> n.sp.	x	-	-	-	this paper
" <i>Euvola</i> " piconus (Ihering, 1907)	-	-	x	-	[2] Fig.4
<i>Paranomia</i> sp.	x	-	-	-	this paper
<i>Pseudolimnea</i> sp.	x	-	-	-	this paper
<i>Acesta latens</i> (Feruglio, 1936b)	x	-	x	-	[4] Pl.25, figs.1-2
<i>Pycnodonte (Phygraea) burckhardtii</i> (Böhm, 1903)	x	-	x	-	[12] Fig.4. A-C; [15] Fig.10.1-2
<i>Pycnodonte (Phygraea) sarmientoi</i> Casadío, 1998	x	x	-	-	[10] Figs.3.1-3.5
<i>Gryphaostrea calophylla</i> (Ihering, 1903)	x	-	x	-	[1] Pl.1, fig.3; [10] Pl.1, figs.1-8; [12] Fig.10.3-4
<i>Turkostrea argentina</i> Griffin et al (2005)	x	-	-	-	[11] Figs.5.A-J;6.A-G
<i>Cubitostrea ameghinoi</i> (Ihering, 1902)	x	x	x	-	[10] Pl. 2, figs 8-15; [12] Fig.11.14-15
<i>Cubitostrea neuquena</i> (Ihering, 1907)	x	x	x	-	[2] Figs 3.a-c; [4] Pl.25, figs 22a-b; [10] Pl.2, figs.1-7
Lucinidae gen. B	x	x	-	-	[2] Pl.3, fig.16 (= <i>Tellina burmeisteri</i> Ihering); [15] Fig.11. 10-11,13
Lucinidae gen. A	x	-	-	-	this paper
" <i>Phacoides</i> " <i>rocana</i> Ihering, 1907	x	x	x	-	[2] Pl.3, fig.15
? <i>Astarte venatorum</i> Wilckens, 1905	-	x	-	x	[21] Pl. 6, fig.7
<i>Claibornicardia paleopatagonica</i> (Ihering, 1903)	-	x	x	-	[1] Fig.12; [4] Pl.23, figs.28-29; [9] Pl.2 figs.G-H; [20] p.53
<i>Cardites feruglio</i> (Petersen, 1946)	-	x	-	-	[5] Pl.10, figs.3-5
<i>Rotundicardia</i> sp.	-	x	-	-	[9] Pl. 2. fig.I (= <i>G.feruglio</i> Petersen, Pl.19, figs. 3-5)
<i>Venericardia australis</i> Masiuk, 1967	x	x	x	-	[5] Pl.10, figs.3-5; [6] Pl.5, fig.2
<i>Bathytormus chubutensis</i> (Feruglio, 1936b)	-	x	-	-	[4] Pl.24, figs.1-2; [18] Figs.6.2-6.4
? <i>Larma chalcedonica</i> (Ihering, 1903)	-	x	x	-	[1] Fig.18; [4] Pl.24, figs.5-13; [7] Pl.1, figs.11-12

SPECIES	NEUQ.-COLOR.BASIN	C. ASFALTO BASIN	G. SAN JORGE BASIN	AUSTRAL BASIN	REFERENCES
<i>Dosinia burckhardti</i> Ihering, 1907	x	x	-	-	[15] Fig.11.9
<i>Marwickia</i> sp.	-	x	-	-	[5] Pl. 10, figs.6–7
" <i>Marcia</i> " <i>pupillia</i> Feruglio 1936a	-	-	x	-	[3] p. 130
" <i>Mactra</i> " <i>exigua</i> Feruglio 1936a	-	x	-	-	[3] Pl.2, figs.4–5 (= <i>M. impervia</i> Fer.1936b,Pl.24, fig.4)
<i>Carycorbula hatcheri</i> (Ortmann, 1902)	-	-	x	-	[4] Pl.24, fig.15
" <i>Lutraria</i> " <i>ameghinoi</i> Ihering 1907	x	-	-	-	[2] Pl.3, fig 17
" <i>Panopea</i> " <i>patagonica</i> Feruglio 1936b	-	x	x	-	[4] Pl.24, figs.18–20
<i>Panopea plateni</i> Feruglio 1936b	-	-	x	-	[4] Pl.24, figs.21–22
" <i>Panopea</i> " sp. II Feruglio 1936b	-	-	x	-	[4] Pl.24, figs.23–25
<i>Panopea</i> sp.I Feruglio 1936b	-	x	-	x	[4] Pl.24, figs 16–17
<i>Panopea thomasi</i> Ihering	-	x	-	x	[4] Pl.21, figs 10–11; [6] Pl.6, fig. 4
Patellogastropoda indet.	x	x	-	-	this paper
<i>Cidarina lenzaniyeuensis</i> del Río, 2012	-	x	-	-	[16] Figs 3.1–3.3
" <i>Turritella</i> " <i>burckhardti</i> Ihering, 1903	x	x	-	-	[1] Fig.9; [9] Pl.2, fig. A; [15] Fig.11.3
" <i>Turritella</i> " <i>malaspina</i> Ihering, 1903	x	x	x	-	[1] Fig.13; [4] Pl.26, fig.17; [5] Pl.11, fig.23–26; [7] Pl.1, figs.9–10
" <i>Turritella</i> " <i>ameghinoi</i> Ihering, 1903	-	x	x	x	[1] Fig.14; [4] Pl.26, fig.18; [8] Figs.3.2–3.3
Aporrhaidae indet. (= <i>Rostellaria rothi</i> Ihering, 1903)	x	-	-	-	[15] Fig.10.9–10
Aporrhaidae indet. (= <i>R. striatissima</i> Ihering, 1903)	x	x	x	-	[1] Pl.2, fig.16
Aporrhaidae nov.gen	x	x	x	-	this paper
<i>Struthioptera</i> sp.	x	x	-	-	this paper
<i>Astroaporrhais dorotensis</i> Zinsmeister & Griffin 1995	-	-	-	x	[19] Fig.2.17
<i>Perissodonta senoniana</i> (Camacho & Zinsmeister, 1989)	-	-	-	x	[8] Figs.3.4–3.5
<i>Perissodonta</i> sp.	x	-	-	-	this paper
Calyptreidae indet.	x	x	x	-	[4] Pl.26, figs. 14–15
? <i>Spirogalerus</i> cf. <i>S. laevis</i> (Philippi, 1887)	-	-	-	x	[8] Fig.3.6
Globisininae indet.	x	x	-	-	this paper
<i>Tejonia tapiae</i> (Feruglio, 1936b)	-	x	x	-	[4] Pl.26, fig.10; [16] (= <i>Euspira</i> sp.) figs.3.4–3.6
<i>Pseudamaura dubia</i> Petersen, 1946	-	x	-	x	[5] Pl.11, figs. 29–30; [7] Pl.1,figs.14–15; [8] Fig.4.6–4.7; [17] figs.5.1–5.6
<i>Darwinices claudiae</i> Griffin & Pastorino, 2013	-	x	x	x	[8] Figs.4.2–4.3; [17] Fig.16.1–12
<i>Prisofiscus</i> cf. <i>P. gracilis</i> (Wilckens, 1905)	x	x	-	-	[16] Figs 3.7–3.8
<i>Cavoscala</i> sp.	-	x	-	-	[16] Figs.3.12–3.15
<i>Gyroscala daniana</i> del Río, 2012	x	x	x	-	[12] Fig.3.E (= <i>Epitonium</i> sp); [16] Figs.3.9–3.11
<i>Acира</i> sp.	-	x	-	-	this paper
<i>Pseudotylostoma romeroi</i> Ihering, 1903	x	x	-	-	[15] Fig.10.7–8
? <i>Pseudotylostoma dubium</i> Feruglio, 1936b	-	-	x	-	[4] Pl.26, fig.16
<i>Pseudotylostoma</i> sp.	-	-	-	x	[8] Figs.4.10–4.11
Buccinidae gen.nov.A	-	x	x	-	this paper
Buccinidae gen.nov.B	-	-	x	-	this paper
Buccinidae gen.nov.C	-	x	x	-	[3] Pl.2, fig.8 (= <i>Cominella iheringi</i> Feruglio, 1936a)
Buccinidae gen. nov. D	-	x	x	-	this paper
<i>Austrophaera patagonica</i> (Feruglio, 1936b)	-	x	-	-	[4] Pl.26, figs.11–13; [5] Pl.11, fig. 20; [16] Figs.3.16–3.17
<i>Austrophaera</i> sp.	-	-	-	x	[8] Figs.5.2–5.6 (<i>non Cominella patagonica</i> Feruglio 1936b)
" <i>Pseudofax</i> " <i>costellatus</i> Griffin & Hünicken, 1994	-	-	-	x	[8] Figs. 5.7–5.8
<i>Fusinus</i> sp.	x	x	-	-	[16] Figs.4.1–4.3
<i>Rocalaria alani</i> del Río, 2012	x	x	-	-	[16] Figs.4.4–4.7
<i>Taioma</i> sp. A	-	-	-	x	this paper
<i>Taioma</i> sp. B	x	x	x	-	this paper
<i>Microfulgur concheyroae</i> del Río, 2012	x	x	x	-	[16] Figs.5.6–5.10
<i>Fyfea beui</i> Griffin & Hünicken 1994	-	x	x	x	[8] Figs.7.3–7.6
<i>Heteroterma carmeloii</i> del Río, 2012	-	x	-	-	[16] Figs.5.1–5.6

SPECIES					REFERENCES
	NEUQ.-COLOR.BASIN	C. ASFALTO BASIN	G. SAN JORGE BASIN	AUSTRAL BASIN	
<i>Heteroterma elegans</i> Griffin & Hünicken, 1994	-	-	-	x	[8] Figs.7.1-7.2 [4] Pl.21,fig.14 (= <i>Cominella precursor</i> Wilckens, 1905)
<i>Heteroterma</i> n.sp	-	x	-	-	
<i>Sulcobuccinum prominentum</i> del Río, 2012	x	x	x	-	[5] Pl.11, fig.21; [16] Figs.6.1-6.7
<i>Harpidae</i> nov.gen.	-	x	-	-	this paper
<i>Volutidae</i> indet.	-	x	x	-	this paper
? <i>Zemacies</i> cf. ? <i>Z. crassatina</i> (Feruglio,1936b)	-	-	x	x	[4] P.26, fig.10; [8] Figs.7.7-7.8
<i>Cancellariidae</i> indet.	-	-	x	-	this paper
" <i>Tornatellaea</i> " sp.	x	-	-	x	[8] Figs.8.3-8.4
<i>Crenilabium (Eoacteon)</i> sp.	-	x	x	x	[8] Figs.8.1-8.2 (" <i>Tornatellaea</i> " cf. " <i>T."morbosa</i> Fin.& Marw.1937)
<i>Ringiculidae</i> sp.	-	x	-	-	this paper
<i>Priscaphander</i> sp.A	x	-	x	-	[12] Fig.3.J
<i>Priscaphander</i> cf. <i>sanjoesensis</i> Griffin & Hünicken, 1994	-	-	x	-	[8] Figs.8.8-8.9
<i>Priscaphander braccaccini</i> Griffin & Hünicken, 1994	-	-	-	x	[8] Figs.8.10-8.13
<i>Scaphander</i> sp. Griffin & Hünicken, 1994	-	-	-	x	[8] Fig.8.7

Appendix 2. Presence/absence of Paleocene genera in Southern Hemisphere. Genera of Antarctica (Sobral and Lopez de Bertodano Formations) compiled from Stilwell et al. (2004) and Beu (2009); New Zealand (1) (Wangaloan, Kauru, Broken River, Waipawa Shale, and Abbotsford formations), compiled from Beu and Raine (2009) and Stilwell (2003); New Zealand (2) (Kaiwhata River); Australia (Peeble Point, Dilwyn, Cardinia Calcarenite King Park formations); Chatham Islands (Red Bluff Tuff), compiled from Stilwell (op.cit.); genera of Argentinean Danian basins: this work.

AGE	Early Danian					
	PATAGONIAN BASINS				ANTARCTICA	
BASINS	NEUQ.-COLOR.	C. ASFAUTO	G.SAN JORGE	AUSTRAL	NEW ZEALAND (1)	LATE DANIAN
					NEW ZEALAND (2)	SELANDIAN-THANETIAN
					AUSTRALIA	CHATHAM ISLAND
						THANETIAN
<i>Nucula</i>	0	1	1	0	1	0
<i>Leionucula</i>	1	1	1	1	1	0
<i>Lamellinucula</i>	0	0	0	0	0	1
<i>Austronucula</i>	0	0	0	0	0	1
<i>Linucula</i>	0	0	0	0	1	0
? <i>Varinucula</i>	0	0	0	0	0	1
<i>Comiteleda</i>	0	0	0	0	0	1
<i>Jupiteria</i>	0	0	0	0	1	1
<i>Sacella</i>	1	1	1	0	0	0
<i>Nuculana</i>	1	0	0	0	0	0
<i>Sarepta</i>	0	0	0	0	0	1
<i>Ledina</i>	0	1	1	0	1	0
<i>Nemodon</i>	1	0	0	0	0	0
<i>Yoldia (Calohardia)</i>	1	1	1	0	0	0
<i>Spineilo</i>	0	1	0	0	1	0
<i>Neilo</i>	1	1	0	1	0	1
<i>Arca</i>	1	0	1	0	0	1
<i>Barbatia</i>	0	0	1	0	0	0
<i>Quadrilatera</i>	0	0	0	0	0	0
<i>Cucullaea</i>	1	1	0	1	0	0
<i>Limopsis</i>	0	0	0	0	0	1
<i>Limopsisista</i>	0	0	0	0	1	0
<i>Glycymeris</i>	1	1	1	0	0	0
<i>Gregariella</i>	1	0	1	0	0	0
? <i>Septifer</i>	0	0	0	0	1	0
? <i>Hormomya</i>	0	0	0	0	0	1
? <i>Atrina</i>	1	0	0	0	0	0
<i>Pinna</i>	1	1	0	0	1	0
<i>Plicatula</i>	1	0	0	0	0	0
<i>Electroma (Pterelectroma)</i>	0	0	0	0	1	0
<i>Isognomon</i>	0	0	0	0	1	0
<i>Parvamussium</i>	1	0	0	0	0	1
? <i>Cycloclamys</i>	0	0	0	0	0	1
? <i>Mesopeplum</i>	0	0	0	0	0	0
<i>Chlamys</i>	0	0	0	0	1	0
<i>Serripecten</i>	0	0	0	0	0	0
<i>Talochlamys</i>	1	1	1	0	0	0
<i>Delectopecten</i>	1	0	0	0	0	1
<i>Eburneopecten</i>	1	0	0	0	0	0
" <i>Euvola</i> "	0	0	1	0	0	0
<i>Paranomia</i>	1	0	0	0	0	0
<i>Anomia</i>	0	0	0	0	1	0
<i>Spondylus</i>	0	0	0	0	0	1
<i>Limea (Pseudolimea)</i>	1	0	0	0	0	0
<i>Lima</i>	0	0	0	0	1	0
<i>Limatulella</i>	0	0	0	0	0	1
<i>Notolimea</i>	0	0	0	0	0	1
<i>Ctenoides</i>	0	0	0	0	0	0
<i>Acesta (Acesta)</i>	1	0	1	0	0	1
<i>Seymourtula</i>	0	0	0	1	0	0
<i>Ostrea</i>	0	0	0	1	0	0

AGE	Early Danian					
	PATAGONIAN BASINS				ANTARCTICA	
BASINS	NEUQ.-COLOR.	C. ASFAUTO	G.SAN JORGE	AUSTRAL	NEW ZEALAND (1)	LATE DANIAN
					NEW ZEALAND (2)	SELANDIAN-THANETIAN
					AUSTRALIA	CHATHAM ISLAND
						THANETIAN
<i>Pycnodonte (Phygraea)</i>	1	1	1	0	0	0
<i>Gryphaostrea</i>	1	0	1	0	0	0
<i>Cubitostrea</i>	1	1	1	0	0	0
<i>Turkostrea</i>	1	0	0	0	0	0
<i>Pycnodonte (?Notostrea)</i>	0	0	0	0	1	0
<i>Crenostrea</i>	0	0	0	0	0	0
<i>Eotrigonia</i>	0	0	0	0	0	1
<i>Pteromyrtea</i>	1	1	0	0	1	0
" <i>Phacooides</i> "	1	1	1	0	0	0
<i>Lucinidae gen A</i>	1	0	0	0	0	0
<i>Lucinidae gen B</i>	1	1	0	0	0	0
<i>Lucinoma</i>	0	0	0	0	1	0
<i>Miltha</i>	0	0	0	0	1	0
<i>Myrtea</i>	0	0	0	0	0	1
? <i>Jagolucina</i>	0	0	0	0	0	1
<i>Felaniella (Zemysia)</i>	0	0	0	0	0	1
<i>Thyasira</i>	0	0	0	0	1	1
<i>Bornia</i>	0	0	0	0	0	1
? <i>Kellia</i>	0	0	0	0	1	0
<i>Cyamiocardium</i>	0	0	0	0	0	1
? <i>Astarte</i>	0	1	0	1	0	0
<i>Claibornicardia</i>	0	1	1	0	0	0
<i>Cardites</i>	0	1	0	0	0	0
<i>Venericardia</i>	1	1	1	0	0	0
<i>Rotundicardia</i>	0	1	0	0	0	1
<i>Glyptactis (Fasciculidaria)</i>	0	0	0	0	0	0
<i>Purpurocardia</i>	0	0	0	0	1	0
<i>Carditellopsis</i>	0	0	0	0	0	1
<i>Bathytormus</i>	0	1	0	0	0	0
<i>Nemocardium (Pratulum)</i>	0	0	0	0	1	0
<i>Lahillia</i>	0	0	0	0	1	1
<i>Maorimactra</i>	0	0	0	0	1	0
<i>Mactra</i>	0	0	0	0	0	0
<i>Bertinella</i>	0	0	0	0	0	1
<i>Elliptotellina</i>	0	0	0	0	0	0
<i>Gari</i>	0	0	0	0	1	0
? <i>Corbicula</i>	0	0	0	0	0	1
? <i>Larma</i>	0	1	1	0	0	0
<i>Marwickia</i>	0	1	0	0	1	0
<i>Aphrodina (Tikia)</i>	0	0	0	0	1	0
? <i>Dosinia</i>	1	1	0	0	0	0
<i>Dosinia ?(Kereia)</i>	0	0	0	0	1	0
<i>Dosinobia</i>	0	0	0	0	0	1
<i>Cyclorismina</i>	0	0	0	1	0	0
<i>Caryocorbula</i>	0	0	1	0	0	1
<i>Panopea</i>	0	1	1	1	1	0
" <i>Lutraria</i> "	1	0	0	0	0	0
<i>Pholadidea?</i>	0	0	0	0	0	1
c.f. <i>Laternula</i>	0	0	0	0	0	1
<i>Periploma</i>	0	0	0	1	0	0
<i>Haliris</i>	0	0	0	0	0	1

AGE	Early Danian						Late Danian	Selandian-Thanetian	Thanetian
	PATAGONIAN BASINS			ANTARTICA	NEW ZEALAND (1)	NEW ZEALAND (2)			
BASINS	NEUQ.-COLOR.	C. ASFALTO	G.SAN JORGE			AUSTRAL	CHATHAM ISLAND		
<i>Cuspidaria</i>	0	0	0	0	0	0	0	1	1
<i>Verticordia</i>	0	0	0	0	0	0	0	1	0
<i>Patellogastropoda</i> indet.	1	1	0	0	0	0	0	0	0
<i>Perotrochus</i>	0	0	0	0	0	0	0	0	1
<i>Conotomaria</i>	0	0	0	0	1	0	0	0	0
? <i>Chelotia</i>	0	0	0	0	0	0	0	0	1
<i>Anatoma</i>	0	0	0	0	0	0	0	0	1
<i>Scissurella</i>	0	0	0	0	0	0	0	0	1
<i>Emarginula</i>	0	0	0	0	0	0	0	1	1
<i>Rimula</i>	0	0	0	0	0	0	0	1	0
<i>Puncturella</i>	0	0	0	0	0	0	0	1	0
? <i>Cocculina</i>	0	0	0	0	0	0	0	1	0
<i>Lissosteta</i>	0	0	0	0	0	0	0	0	1
<i>Skenea</i>	0	0	0	0	0	0	0	0	1
<i>Margarella</i>	0	0	0	0	0	0	0	0	1
<i>Calliotropis</i>	0	0	0	0	0	0	0	1	0
<i>Bathymophilida</i>	0	0	0	0	0	0	0	1	0
<i>Botelloides</i>	0	0	0	0	0	0	0	1	0
<i>Cidarina</i>	0	1	0	0	0	0	0	0	0
<i>Conominolia</i>	0	0	0	0	0	1	0	1	0
<i>Calliostoma</i>	0	0	0	0	0	0	0	0	1
<i>Bathybembix</i>	0	0	0	0	0	0	0	0	1
<i>Calliolarica</i>	0	0	0	0	0	0	0	0	1
<i>Bittiscala</i>	0	0	0	0	0	1	0	0	0
<i>Bolma</i> (<i>Ormastralium</i>)	0	0	0	0	0	1	0	0	0
<i>Guildfordia</i> ?(<i>Opella</i>)	0	0	0	0	0	0	0	1	0
<i>Cirsochilus</i>	0	0	0	0	0	0	0	1	0
? <i>Parauchelus</i>	0	0	0	0	0	0	0	1	0
<i>Littorina</i>	0	0	0	0	1	0	0	0	0
? <i>Bittium</i>	0	0	0	0	1	0	0	0	0
<i>Pareora</i>	0	0	0	0	0	0	0	0	1
<i>Turritellidae</i> nov. gen.	1	1	1	1	0	0	0	0	0
<i>Colpopsigma</i>	0	0	0	0	0	0	0	1	0
<i>Spiricolpus</i>	0	0	0	0	0	1	0	0	0
<i>Zeacolpus</i>	0	0	0	0	0	1	0	0	1
<i>Circulus</i>	0	0	0	0	0	0	0	1	0
<i>Aporrhaidae</i> nov. gen.	1	1	1	0	0	0	0	0	0
<i>Aporrhaidae</i> indet.	1	1	1	0	0	0	0	0	0
<i>Austroaporrhais</i>	0	0	0	1	0	0	0	0	0
<i>Struthioptera</i>	1	1	0	0	0	1	0	0	0
<i>Struthiochenopus</i>	0	0	0	0	1	0	0	0	0
<i>Drepanocheilus</i> (<i>Tulochilus</i>)	0	0	0	0	0	1	0	1	0
n.gen. aff. <i>Hemichenopus</i>	0	0	0	0	0	1	0	0	0
<i>Perissodonta</i>	1	0	0	1	1	1	0	0	0
<i>Conchotyra</i>	0	0	0	0	0	1	0	0	0
<i>Calyptaeidae</i> indet.	1	1	1	0	0	0	0	0	0
<i>Cheilea</i>	0	0	0	0	0	0	0	0	1
? <i>Spirogalerus</i>	0	0	0	1	0	1	0	0	0
? <i>Cypraeidae</i>	0	0	0	0	0	0	0	0	1
? <i>Notadusta</i>	0	0	0	0	0	0	0	0	1
<i>Bernaya</i>	0	0	0	0	0	0	0	0	1

AGE	Early Danian						Late Danian	Selandian-Thanetian	Thanetian
	PATAGONIAN BASINS			ANTARTICA	NEW ZEALAND (1)	NEW ZEALAND (2)			
BASINS	NEUQ.-COLOR.	C. ASFALTO	G.SAN JORGE			AUSTRAL	CHATHAM ISLAND		
<i>Zoila</i>	0	0	0	0	0	0	0	0	1
<i>Ovulidae?</i>	0	0	0	0	0	0	0	0	1
<i>Globisininae</i> indet.	1	1	0	0	0	0	0	0	0
<i>Globisimum</i>	0	0	0	0	0	1	0	0	0
<i>Tejonia</i>	0	1	1	0	0	0	0	0	0
<i>Pseudamaura</i>	0	1	0	1	0	0	0	0	0
<i>Magnatica</i> (<i>Spelanacea</i>)	0	0	0	0	0	1	0	0	0
<i>Taniella</i>	0	0	0	0	0	1	0	0	0
<i>Amauropsona</i>	0	0	0	0	0	1	0	0	0
<i>Amauroopsis</i>	0	0	0	0	0	1	0	0	0
? <i>Amauroopsis</i>	0	0	0	0	1	0	0	0	0
<i>Euspira</i>	0	0	0	0	0	1	0	1	0
<i>Polinices</i> (<i>Polinices</i>)	0	0	0	0	0	1	0	0	0
<i>Polinella</i>	0	0	0	0	0	0	1	0	0
<i>Eunaticina</i>	0	0	0	0	0	1	0	0	0
<i>Darwinices</i>	0	1	1	1	0	1	0	0	0
<i>Galeoidea</i>	0	0	0	0	0	0	0	1	0
<i>Taieria</i>	0	0	0	0	0	1	0	0	1
<i>Antarctiranella</i>	0	0	0	0	1	0	0	0	0
<i>Sassia</i> (<i>Sassia</i>)	0	0	0	0	0	0	0	1	1
<i>Kotakaia</i>	0	0	0	0	0	0	0	0	1
<i>Priscifucus</i>	1	1	0	0	0	1	0	0	0
<i>Cerithiella</i>	0	0	0	0	0	0	0	1	0
<i>Eulimidae</i>	0	0	0	0	0	0	0	0	1
<i>Melanella</i>	0	0	0	0	0	1	0	0	0
<i>Nisso</i>	0	0	0	0	0	1	0	0	0
<i>Epitoniiidae</i>	0	0	0	0	0	0	0	0	1
<i>Opalia</i> (<i>Pliciscala</i>)	0	0	0	0	0	0	0	1	0
<i>Cavoscala</i>	0	1	0	0	0	0	0	0	0
<i>Gyroscala</i>	1	1	1	0	0	0	0	0	0
<i>Cirsotrema</i> (<i>Tioria</i>)	0	0	0	0	0	0	0	0	1
<i>Acirsa</i>	0	1	0	0	0	0	0	0	0
<i>Acirsa</i> (<i>Plesioasirsa</i>)	0	0	0	0	0	1	0	0	0
<i>Acirsa</i> (<i>Notoacirsa</i>)	0	0	0	0	0	1	0	0	0
<i>Amaea</i>	0	0	0	0	0	1	0	0	1
<i>Pseudotylostoma</i>	1	1	1	1	0	0	0	0	0
<i>Buccinidae</i> gen.A	0	1	1	0	0	0	0	0	0
<i>Buccinidae</i> gen.B	0	0	1	0	0	0	0	0	0
<i>Buccinidae</i> gen.C	0	1	1	1	0	0	0	0	0
<i>Buccinidae</i> gen.D	0	1	1	0	1	0	0	0	0
<i>Buccinade</i> nov.gen	0	0	0	0	1	0	0	0	0
? <i>Probüccinum</i>	0	0	0	0	1	0	0	0	0
<i>Levifusus</i>	0	0	0	0	0	0	0	1	0
<i>Buccinulum</i>	0	0	0	0	0	1	0	0	0
<i>Penion</i>	0	0	0	0	0	1	0	0	0
<i>Aeneator</i>	0	0	0	0	0	1	0	0	0
<i>Austrocominella</i>	0	0	0	0	1	0	0	0	0
<i>Astrofusus</i>	0	0	0	0	1	0	1	0	1
<i>Nassicola</i>	0	0	0	0	0	1	1	0	0
<i>Austrophaera</i>	0	1	0	1	1	0	0	0	0
" <i>Pseudofax</i> "	0	0	0	1	1	0	0	0	0

AGE	Early Danian						Late Danian	Selandian-Thanetian	Thanetian
	PATAGONIAN BASINS				ANTARTICA	NEW ZEALAND (1)	NEW ZEALAND (2)	AUSTRALIA	CHATHAM ISLAND
BASINS	NEUQ.-COLOR.	CASFALTO	G.SAN JORGE	AUSTRAL					
<i>Pseudofax</i>	0	0	0	0	1	0	0	1	0
<i>Nassaria</i>	0	0	0	0	0	0	0	1	0
<i>Fusinus</i>	1	1	0	0	0	0	0	1	0
<i>Rocalaria</i>	1	1	0	0	0	0	0	0	0
<i>Falsicolus</i>	0	0	0	0	0	0	0	0	1
<i>Paleosephaea</i>	0	0	0	0	1	1	0	0	0
<i>Taioma</i>	1	1	1	1	1	1	0	0	0
<i>Columbarium</i>	0	0	0	0	0	1	1	1	0
<i>Heteroterna</i>	0	1	0	1	1	1	0	0	0
<i>Fyfea</i>	0	1	1	1	0	1	0	0	0
<i>Microfulgur</i>	1	1	1	0	1	1	0	1	0
<i>Pyropsis</i>	0	0	0	0	0	1	0	1	0
<i>Tudiclana</i>	0	0	0	0	0	1	0	0	0
<i>Uttleya</i>	0	0	0	0	0	1	0	0	0
<i>Sulcobuccinum</i>	1	1	1	0	0	0	0	1	0
<i>Volutomitra</i>	0	0	0	0	1	1	0	1	1
<i>Microvoluta</i>	0	0	0	0	0	0	0	1	0
<i>Mitra</i>	0	0	0	0	0	0	0	1	0
<i>Proximitra</i>	0	0	0	0	0	0	0	1	0
<i>Harpidae</i> n.gen.	0	1	0	0	0	0	0	0	0
<i>Volutidae</i>	0	1	1	0	0	0	0	0	0
<i>Volutidae</i> n.gen.	0	0	0	0	0	1	0	0	0
<i>Athleta</i>	0	0	0	0	0	0	0	1	0
<i>Teremelon</i>	0	0	0	0	0	0	0	0	1
<i>Paleomelon</i>	0	0	0	0	1	0	0	0	0
<i>Alcithoe</i>	0	0	0	0	0	1	0	0	0
<i>Austrotoma</i>	0	0	0	0	0	1	0	0	0
<i>Marshalaria</i>	0	0	0	0	0	1	0	1	0
<i>Amuletum</i>	0	0	0	0	0	1	0	0	0
<i>Turrinae</i> nov. gen.	0	0	0	0	0	0	0	0	1
<i>Amaea</i>	0	0	0	0	0	0	0	0	1
<i>Compylacrum</i>	0	0	0	0	0	1	0	0	0
? <i>Zemacies</i>	0	0	1	1	0	1	0	1	1
<i>Cosmasyrinx</i> (<i>Tholitoma</i>)	0	0	0	0	1	1	0	1	0
<i>Cosmasyrinx</i>	0	0	0	0	0	1	0	0	0
<i>Hesperiturris</i>	0	0	0	0	0	1	0	0	0

AGE	Early Danian						Late Danian	Selandian-Thanetian	Thanetian
	PATAGONIAN BASINS				ANTARTICA	NEW ZEALAND (1)	NEW ZEALAND (2)	AUSTRALIA	CHATHAM ISLAND
BASINS	NEUQ.-COLOR.	CASFALTO	G.SAN JORGE	AUSTRAL					
? <i>Insolentia</i>	0	0	0	0	0	0	0	0	1
<i>Inquisitor</i>	0	0	0	0	0	0	1	0	0
<i>Tomopleura</i>	0	0	0	0	0	0	1	0	0
<i>Eothesbia</i>	0	0	0	0	0	1	0	0	0
<i>Mauidrillia</i>	0	0	0	0	0	0	0	1	0
<i>Cancellaridae</i> indet.	0	0	1	0	0	0	0	0	0
<i>Cancellaridae</i> n.gen et n.sp	0	0	0	0	0	1	0	0	0
<i>Pristimerica</i>	0	0	0	0	0	1	0	0	0
<i>Antepepta</i>	0	0	0	0	0	1	0	0	0
<i>Coptostomella</i>	0	0	0	0	0	1	0	0	0
<i>Bonellitia</i>	0	0	0	0	0	0	0	1	0
<i>Kapu atriton</i>	0	0	0	0	0	0	1	0	0
<i>Acteonidae</i> nov. gen.	0	0	0	0	0	1	0	0	0
" <i>Leucotina</i> "	0	0	0	0	0	0	0	0	1
" <i>Tornatellaea</i> "	1	0	0	1	0	1	1	0	0
<i>Tenuiactione</i>	0	0	0	0	0	0	0	1	0
<i>Acteon</i>	0	0	0	0	0	1	0	1	0
<i>Ongleya</i>	0	0	0	0	0	1	1	0	0
<i>Wangacteon</i>	0	0	0	0	0	1	0	0	0
<i>Crenilabium</i>	0	0	0	0	0	1	0	0	0
<i>Crenilabium</i> (<i>Eoacteon</i>)	0	1	1	1	0	0	0	0	0
<i>Ringiculidae</i>	0	1	0	0	0	0	0	0	0
<i>Superstes</i>	0	0	0	0	0	1	0	1	0
<i>Gilbertina</i>	0	0	0	0	0	0	0	1	0
<i>Cylchinanria</i>	0	0	0	0	0	1	0	1	0
<i>Priscaphander</i>	1	0	1	1	0	1	0	1	0
<i>Scaphander</i>	0	0	0	1	0	0	0	0	0
<i>Wangaloa</i>	0	0	0	0	0	1	0	0	0
<i>Eomathilda</i>	0	0	0	0	0	1	0	0	0
<i>Tuba</i>	0	0	0	0	0	0	0	1	0
<i>Gegania</i>	0	0	0	0	0	1	0	0	0
<i>Odostomia</i>	0	0	0	0	0	1	0	1	0
<i>Pyramidella</i>	0	0	0	0	0	1	0	0	0
<i>Raulinia</i>	0	0	0	0	0	0	0	1	0
<i>Spiratella</i>	0	0	0	0	0	0	0	1	1

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