

# New fossil record of Lactoridaceae in southern South America: a palaeobiogeographical approach

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Lactoridaceae are a monotypic family confined to Masatierra Island, Juan Fernández Archipelago, in the Pacific Ocean. It grows in the understorey of a subtropical montane rain forest. Lactoridaceae most probably originated in southern South Africa in the Cretaceous, with the oldest records in the Turonian–Campanian, and reached its widest palaeogeographical distribution by the Maastrichtian, extending into Australia, India, Antarctica, and North and South America. In this paper, we report a new fossil find of lactoridaceous tetrads from the early Miocene of eastern Patagonia, southern South America. This record is the youngest and geographically one of the closest to the extant *Lactoris* distribution area. Patagonian fossil material shows greater similarities to extant *L. fernandeziana* Phil. than to any other described morphotaxon. The family may have migrated into South America, either via Africa (through the Atlantic Ocean) or Antarctica, by the Maastrichtian, growing in eastern Patagonia up to the early Miocene. Arid conditions established in this region by the middle–late Miocene onwards would have determined the restriction of forests to the western lands. Lactoridaceae may have followed a similar migration pattern towards the Pacific coast of South America. The shifting of Lactoridaceae towards Masatierra Island would have occurred in the last 4 Myr by long-distance dispersal events (perhaps by birds). © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 158, 41–50.

ADDITIONAL KEYWORDS: early Miocene – *Lactoris* type – migratory routes – Patagonia – pollen tetrads.

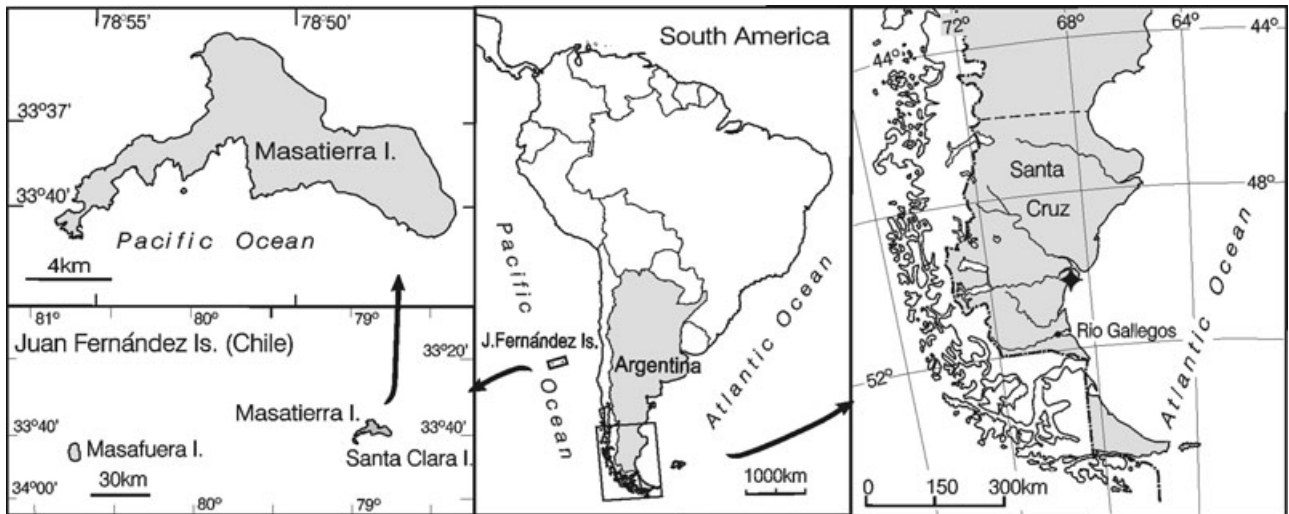
## INTRODUCTION

Lactoridaceae are a monotypic family of shrubby angiosperms represented by a lone species: *Lactoris fernandeziana* Phil. It is the only angiosperm family confined to an oceanic island, Masatierra Island (= Robinson Crusoe), 667 km west of continental Chile (33°40'S and 78–81°W), in the Pacific Ocean (Fig. 1). The island belongs to the volcanic Chilean archipelago of Juan Fernández (Stuessy *et al.*, 1998), formed by two major islands, Masatierra (to the east) and Masafuera (= Alejandro Selkirk Island, to the west), and a third small island, Santa Clara. Lactoridaceae are a family facing extinction and, at present, only 1000 plants are known to exist (Stuessy *et al.*, 1998). Lactoridaceae have a mix of primitive and specialized features, so that, for many years, there has been controversy about their position within

'primitive' orders of subclass Magnoliidae (Sampson, 1995; Stuessy *et al.*, 1998; Bernardello *et al.*, 1999). Currently, there is considerable support for the idea that Lactoridaceae form part of an early-branching of angiosperms, pertaining to the 'palaeoherbs', an informal name defined by Donoghue & Doyle (1989) (in Tucker & Douglas, 1996; Igersheim & Endress, 1998) for a herbaceous group of early-branching angiosperm families. The Angiosperm Phylogeny Group II system (2003) assigned Lactoridaceae to the order Piperales, in the magnoliid clade. Cladistic, morphological, and nucleotide data suggest a close alliance with Aristolochiales (Qiu *et al.*, 1993; Endress, 1994; Igersheim & Endress, 1998; Doyle & Endress, 2000); however, some authors consider its placement in an independent order Lactoridales (Dahlgren, 1983) or even in a superorder (Takhtajan, 1996).

Although, at present, Lactoridaceae are confined to an oceanic island, the fossil record shows that the family had a wider palaeogeographical distribution,

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**Figure 1.** Location map showing the extant distribution of *Lactoris fernandeziana* Phil. (left) and the site containing the fossil tetrads (right).

especially during the Late Cretaceous. Fossils are restricted to pollen grains, with the oldest records in the early Turonian–Campanian off the south-west coast of Africa (Zavada & Benson, 1987). Other lactoridaceous tetrads have been reported from the Campanian–Maastrichtian of Canada and India (Srivastava, 1968; Prasad, Jain & Mathur, 1995), Maastrichtian of the USA and Antarctica (S. Palamarczuk, pers. comm., University of New York, New York; A. Partridge, pers. comm., Biostrata PTY LTD, Victoria), Maastrichtian?–Danian of central Argentina (Ruiz & Quattrocchio, 1997), and Campanian–early Oligocene of Australia (Macphail, Partridge & Truswell, 1999).

In this paper, we present new fossil pollen tetrads of Lactoridaceae from the early Miocene of Argentina, representing one of the closest records of this group to its current distribution. The importance of this find is enhanced by the position of this family in the angiosperm tree and its rarity. *Lactoris fernandeziana* is an endangered species in particular need of conservation (Bernardello *et al.*, 1999). This find also contributes to the knowledge concerning the past distribution of the family, permitting a more confident formulation of biogeographical hypotheses.

The purposes of this investigation are twofold: (1) to describe new fossil tetrads of Lactoridaceae from Argentina; and (2) to evaluate the biogeographical implications of this find and postulate hypotheses.

#### MATERIAL AND METHODS

Fossil pollen grains were recovered from outcrop samples of the Monte León Formation, at the Monte Entrada and Monte Observación sections, north of the

town of Río Gallegos in coastal Santa Cruz Province (Fig. 1). This marine unit consists of tuffaceous sandstones, fine tuffs, and shell beds with a rich invertebrate fossil fauna. It also yielded diverse palynological assemblages composed of marine and continental elements. Detailed stratigraphical and palynological considerations were reported in Barreda & Palamarczuk (2000). The age of the Monte León Formation is well constrained based on radiometric data;  $^{40}\text{Ar}/^{39}\text{Ar}$  determinations indicate an early Miocene age (19.33 Mya) for this unit (Feagle *et al.*, 1995).

Samples were processed following standard palynological techniques (Barreda & Palamarczuk, 2000). Slides of fossil pollen grains are housed at the palynotheca of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', prefixed BA Pal., under the catalogue numbers 1208 and 1239 (ex CIRGEO Palin.)

Modern pollen grains of *L. fernandeziana* were obtained from polleniferous material of the following voucher specimens, all collected on Masatierra Island, Juan Fernández Archipelago, Chile.

1. Quebrada La Piña (Puerto Francés), *Anderson and Bernardello 2041*, 16.i.1996 (CONC).
2. Corrales de Molina, *Anderson and Bernardello 2055*, 17.i.1996, (CONC), in 70% ethanol.

The polleniferous material was acetolysed in the usual manner (Erdtman, 1960) after previous boiling for 30 s in 3% sodium carbonate. The tetrads were mounted in glycerine jelly, and in two liquid media: Alexander reactive (Alexander 19) and a medium composed of two parts of a saturated solution of  $\text{ZnCl}_2$  in HCl 10% and one part of a 3% solution of cellozise.

Slides of extant material are housed at the palynotheca of the Instituto de Botánica Darwinion (IBODA).

## RESULTS

### EXTANT POLLEN (*LACTORIS FERNANDEZIANA* PHIL.)

*Lactoris* pollen tetrads have been described as having saccus-like structures, formed by the separation of the foot layer and the outer ektexine in the equatorial distal region of each grain (Carlquist, 1964; Zavada & Taylor, 1986; Zavada & Benson, 1987). All of these studies were based on pollen acquired from herbarium material. However, Sampson (1995), analysing pollen obtained from preserved flowers, demonstrated that the sacci were absent and were probably an artefact of drying of the tetrads in herbarium material or in germinating pollen grains. Modern pollen grains analysed in the present study, even from herbarium material, agreed with Sampson's (1995) opinions about the artefactual nature of the sacci. Pollen was obtained from two perfect flowers of the same specimen, one with anthers which had not yet begun to open and the other with anthers that had begun to dehisce and contained numerous pollen tetrads in the internal and external surfaces of the tepals. Pollen tetrads recovered from the first flower are shown in Figure 2, and from the second flower in Figures 3–7. In all of these tetrads, there is no evidence of sacci. However, there is a lesser expansion of the monads in pollen tetrads recovered from anthers which had not yet begun to open. This allows us to infer that pollen tetrads reached their complete development out of the anthers.

### Description

Pollen grains shed in tetrahedral tetrads of the calymmate type (Figs 2–10). Monads subspherical in expanded tetrads, with circular outline. Poorly defined distal apertures, variable in size and shape from lenticular to triangular, square or rhomboidal. Exine sculpture scabrate to microrugulate. In equatorial view, individual grains show folds running in polar directions. Pollen wall composed of an ektexine formed by an inner foot layer and an outer tectal layer (infratectum and tectum); there is no endexine. Tectal and foot layers are not firmly coherent to one another. In the proximal region of each grain, the outer ektexine is absent and only the foot layer is present (Sampson, 1995).

### FOSSIL POLLEN (*LACTORIS* TYPE)

Fossil pollen grains of Lactoridaceae have been named as *Lactoripollenites*, *Achenipollenites*, or *Rosannia*. *Lactoripollenites* (Zavada & Benson, 1987) was defined to include fossil pollen grains retained in

tetrads, similar to those of extant *Lactoris*. However, the distal structure of these grains was misinterpreted as a saccus, as in the case of *Lactoris*. *Achenipollenites*, particularly *A. acheniensis*, was also used to name fossil *Lactoris*-like pollen in industry reports (Macphail *et al.*, 1999). This genus was defined to encompass monoporate pollen grains in tetrads (Kruttsch, 1970), with a wide diagnosis that allows the inclusion of pollen grains with different morphological features. However, recent studies using light microscopy, scanning electron microscopy, and transmission electron microscopy techniques added new characters to the diagnosis that clearly separate *Achenipollenites* from the tetrads of *Lactoris* (Zetter, Hesse & Huber, 2002). *Rosannia*, as *R. manika*, was described as a triporate single grain, related to the triprojectacites complex, and not as a tetrad (Srivastava, 1968). Further observations proved its lactoridaceous affinity (S. Srivastava, pers. comm., University of California). Therefore, the original diagnosis of *Rosannia* should be emended in order to describe the real morphology of the grain. In this condition, *Rosannia* would have priority over *Lactoripollenites*. In this paper, fossil tetrads of Lactoridaceae are informally named as '*Lactoris* type' pending an emended diagnosis of *Rosannia* based on the type material.

### Description

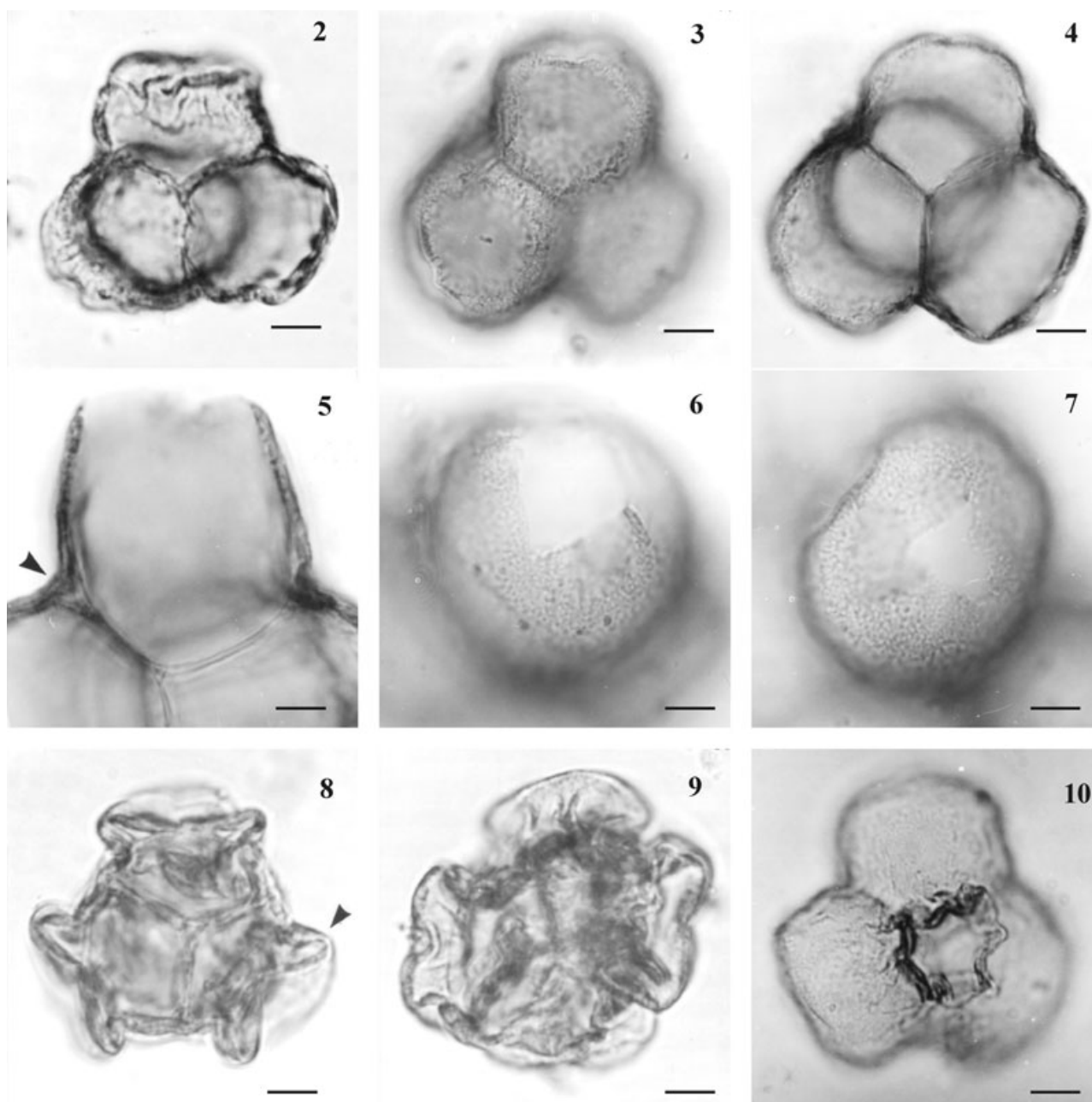
Pollen grains shed in permanent tetrads, radio-symmetric. Individual grains heteropolar with a mushroom-shaped appearance developed by the invagination of the distal face and the separation of the sexine and nexine. Exine of two layers (Figs 11, 12), 1 µm thick. Sexine thicker than nexine, possibly columellate, consisting of a perforate-granulate layer, reaching a microrugulate to plicate appearance at the roots of the mushroom-shaped monads (Figs 13, 14). Sexine continuous around each of the four pollen grains in the tetrad (calymmate type) and absent from the proximal hemisphere of each pollen grain. Nexine very thin, difficult to distinguish, except in the equatorial region of each grain. Distal aperture not clearly defined (Figs 15, 16), perhaps by the action of the fossilization processes.

### Dimensions

Tetrad diameter: 30–32 µm (two specimens measured).

### Comparison

The Patagonian material shows a close resemblance to fossil tetrads of Lactoridaceae, sharing a similar morphology. *Lactoripollenites* from Africa (Zavada & Benson, 1987) and Australia (Macphail *et al.*, 1999) differ in having a thick nexine flooring the

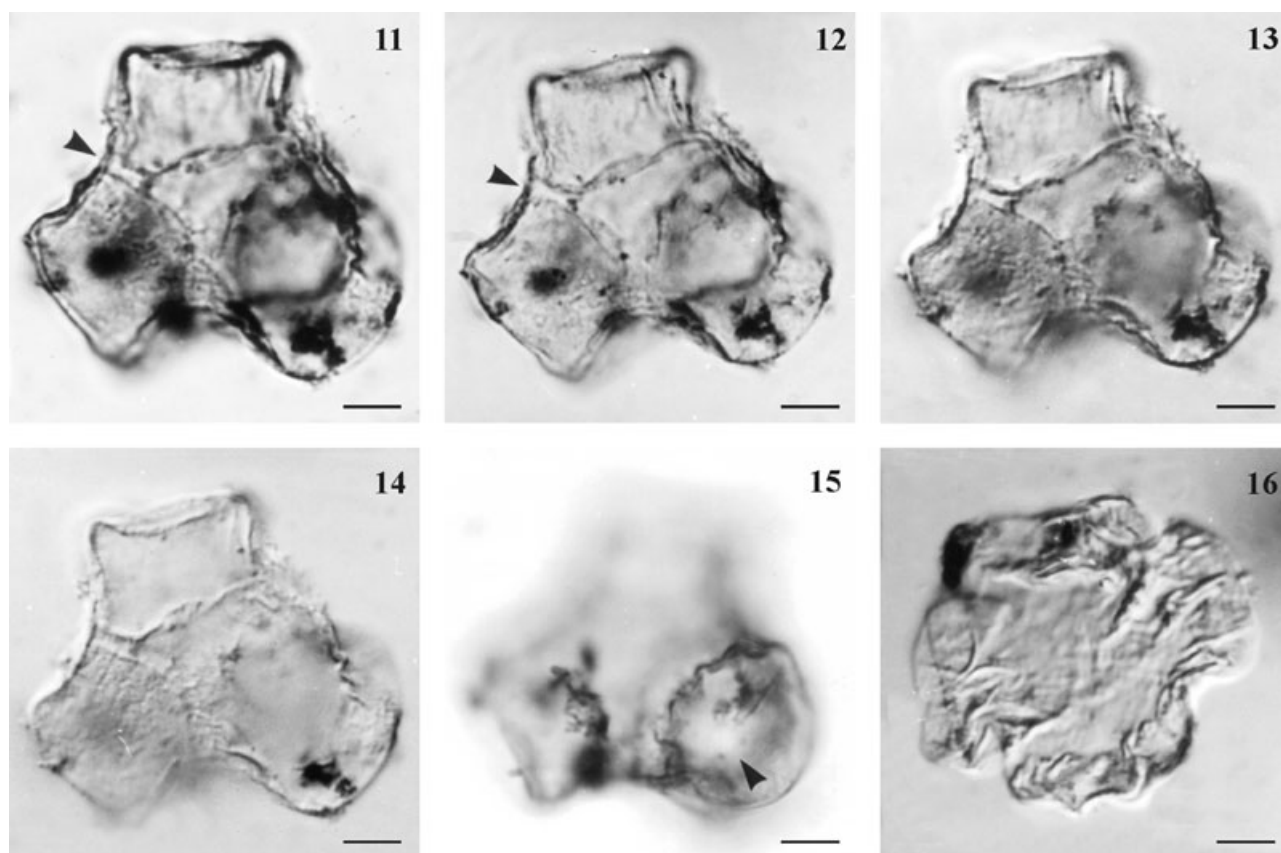


**Figures 2–10.** *Lactoris fernandeziana* Phil. Fig. 2. Semi-expanded tetrad during the anthesis period. Figs 3, 4. General view of an expanded pollen tetrad after pollen has been shed from the anthers. Fig. 3. High focus showing small ridges of sexine. Fig. 4. Optical section. Fig. 5. Detail of a pollen tetrad with a torn distal face; arrow shows separation between sexine and nexine. Fig. 6. Monad showing a quadrangular distal aperture. Fig. 7. Monad showing a triangular distal aperture. Figs 8, 9. Tetrads with aborted cells of saccate appearance. Fig. 10. Tetrad with a small aborted cell. All figures: scale bar, 5  $\mu$ m. All from *Anderson and Bernardello 2041*. Figs 3, 4: in glycerine jelly. Figs 2, 5–10:  $\text{ZnCl}_2$ .

monads. Moreover, the Australian specimens are larger (40–56  $\mu$ m) than our material (30–32  $\mu$ m). *Rosannia manika* Srivastava illustrated from the Maastrichtian?–Danian of central Argentina (Ruiz & Quattrocchio, 1997) and Campanian–Maastrichtian

of India (Prasad *et al.*, 1995) is also very similar. According to the photographs, they share a similar shape, size, and general morphology; however, there are no descriptions, and therefore it was impossible to achieve an accurate comparison.





**Figures 11–16.** *Lactoris* type from the Miocene of Patagonia. Figs 11–15. Pollen tetrad from Monte Observación section at different focus levels. Figs 11, 12. General view; arrows show the separation between sexine and nexine. Figs 13, 14. Differential interference contrast photomicrographs showing the microrugulate sculpture. Fig. 15. Focus on the distal face of a monad showing leptome (arrow). Fig. 16. Poorly preserved specimen from Monte Entrada section with differential interference contrast. All figures: scale bar, 5  $\mu\text{m}$ .

### Discussion

Patagonian Miocene tetrads are close to the extant species *L. fernandeziana* Phil., particularly considering the nexine thickness in the proximal pole of the monads. All described pre-Miocene fossil tetrads have a thicker nexine than both the Patagonian Miocene and recent *Lactoris* tetrads. Pre-Miocene specimens might represent an ancestral type of Lactoridaceae with a more widespread palaeogeographical distribution.

## DISCUSSION AND CONCLUSIONS

### PALAEOENVIRONMENTAL CONSIDERATIONS

Today, *L. fernandeziana* grows in the understorey of the endemic upper montane forest unit of Greimler *et al.* (2002), at altitudes between 340 and 690 m, usually above 500 m. This vegetation zone is windy, foggy, and rain-swept, and *Lactoris* thrives on steep slopes and vertical cliff faces (Bernardello *et al.*, 1999). The climate of the island is subtropical to

temperate, with a rainfall regime of Mediterranean type: wet winters and dry summers (mean annual precipitation, 1000 mm; mean annual temperature, 15 °C) (Mueller-Dombois & Fosberg, 1998). The dominant native forest trees are those of the families Myrtaceae, Winteraceae, Rutaceae, arborescent Asteraceae, and an endemic palm. Tree ferns of Cyatheaceae and Polypodiaceae, other woody plants, many herbaceous ferns, and *Gunnera* species are mainly confined to the understorey (Marticorena, Stuessy & Baeza, 1998; Mueller-Dombois & Fosberg, 1998). Lactoridaceae are vulnerable to disturbance and survive in the most isolated parts of the island (Stuessy *et al.*, 1998).

Ancient Lactoridaceae could have developed in somewhat comparable forests under temperate to warm temperate climatic conditions. Early Miocene floras in south-eastern Patagonia were dominated by forest species of Nothofagaceae, Podocarpaceae, and Araucariaceae, with abundant ferns of Lophosoriaceae, Pteridaceae, and Polypodiaceae. Palms,

**Table 1.** Details of the known fossil records of Lactoridaceae

Location	Bearing deposit	Age	Name used	Reference
South Africa	Orange and Eastern Cape Basins	Turonian–Campanian	<i>Lactoripollenites africanus</i> Zavada & Benson	Zavada & Benson, 1987
Canada	Edmonton Fm./Alberta	Campanian–Maastrichtian	<i>Rosannia manika</i> Srivastava	Srivastava, 1968
USA	Fox Hill Fm./South Dakota	Maastrichtian	Lactoridaceae <i>s.l.</i>	S. Palamarczuk, pers. comm.
Australia	Carnarvon, Arafura, Goats Paddock, Astrobleme, Bonaparte, Gippsland, and Otway Basins and Tasmania	Campanian–early Oligocene	<i>Lactoripollenites</i> sp. cf. <i>L. africanus</i> ; <i>Achenipollenites</i> sp. cf. <i>A. acheniense</i> Krutzsch	Macphail <i>et al.</i> , 1999
India	Krishna-Godavari Basin	Campanian–Maastrichtian	<i>Rosannia manika</i> Srivastava	Prasad <i>et al.</i> , 1995
Antarctic Peninsula	López de Bertodano Fm.	Maastrichtian	Lactoridaceae <i>s.l.</i>	A. Partridge, pers. comm.
Argentina	Pedro Luro Fm./Colorado Basin	Maastrichtian?–Danian	<i>Rosannia manika</i> Srivastava	Ruiz & Quattrocchio, 1997
	Monte León Fm./Austral Basin	Early Miocene	<i>Lactoris</i> type	This paper

Asteraceae (Mutisiinae, *Cnicothamnus* type), Winteraceae, Myrtaceae, Escalloniaceae, and Gunneraceae were also common. Xerophytic formations were also recorded, but they would have occupied coastal salt-marshes and pockets in inland areas (Barreda & Palazzesi, 2007).

#### PALAEOBIOGEOGRAPHICAL CONSIDERATIONS

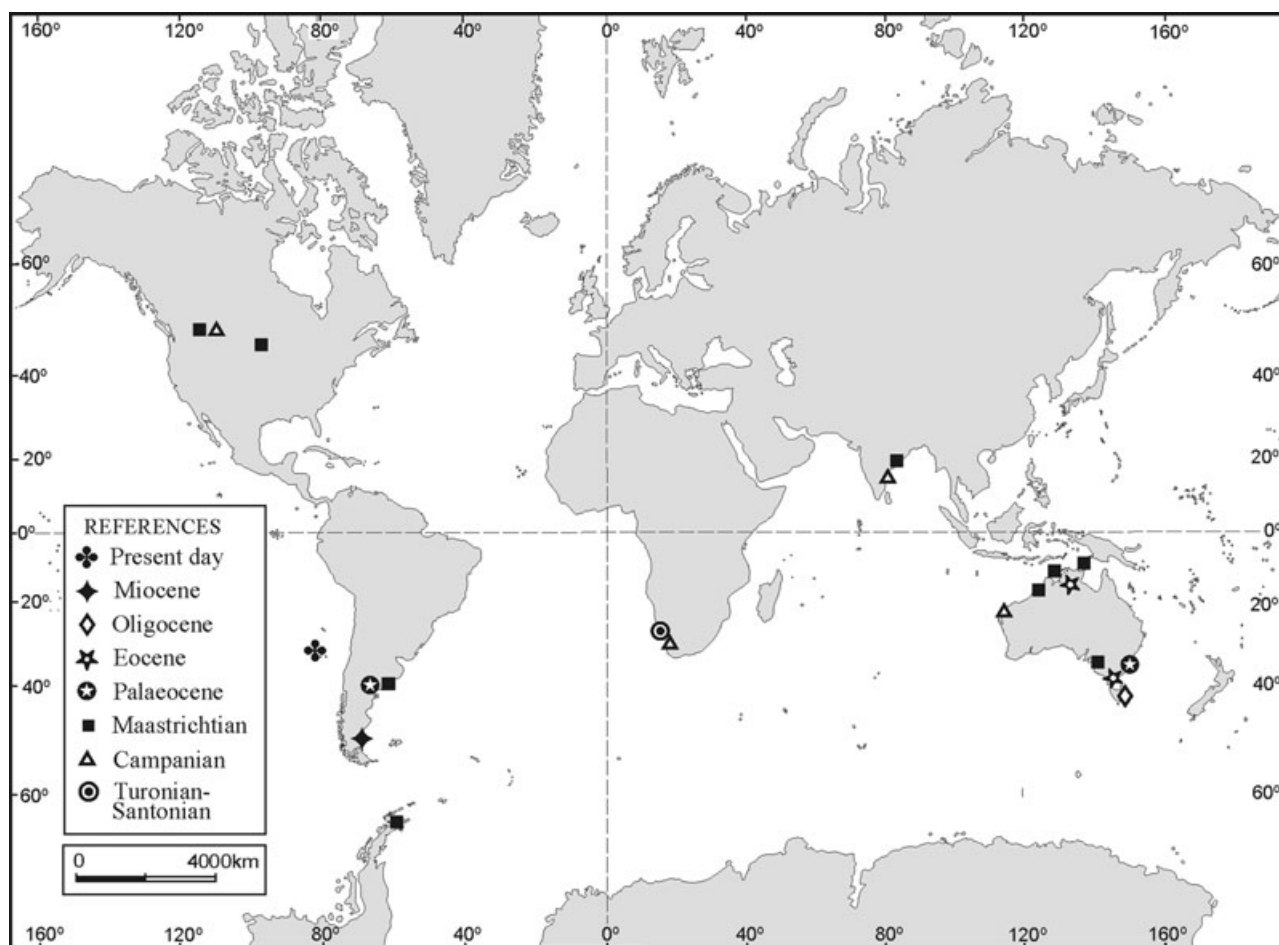
Fossils of Lactoridaceae are still scarce (Table 1), so it is not easy to determine the biogeographical history of the family, which was widespread in the Late Cretaceous, and is now restricted to a volcanic island in the Pacific Ocean.

To date, the only fossil record of Lactoridaceae in southern South America was from the Maastrichtian?–Danian of north-eastern Patagonia (Ruiz & Quattrocchio, 1997). The present find extends the temporal distribution of the Lactoridaceae to the early Miocene. This record is the youngest and geographically one of the closest to the extant *Lactoris* distribution area (at about 2000 km south-east of Masatierra Island).

Lactoridaceae may have originated in South Africa during the Cretaceous, where it evolved (Macphail *et al.*, 1999) and migrated into Australia, North America, India, Antarctica, and South America before the end of this period (Fig. 17). Migration from Africa to other remaining Gondwanan continents may have

been possible, considering the relative proximity of these landmasses. Dispersal to North America, on the contrary, is intriguing, and migratory routes are difficult to explain on the basis of the present knowledge. Routes of dispersion of Lactoridaceae from Africa to Australia have been discussed extensively by Macphail *et al.* (1999). The South American route, which is the major interest of this study, may have occurred in at least three ways: (1) direct migration from Africa to South America via the Atlantic Ocean during the Late Cretaceous; (2) migration from Antarctica into southern South America during the Maastrichtian; (3) migration from North America into South America, also during the Maastrichtian. We briefly discuss these three hypotheses, which are not mutually exclusive.

By the time of the first discovery of Lactoridaceae on the southern coast of Africa (Turonian–Campanian, *c.* 93–76 Mya), southern South America and Africa were separated by an already wide Atlantic Ocean (Coetzee, 1993; Pitman *et al.*, 1993). However, marine barriers have not always hindered plant migrations (Mueller-Dombois & Fosberg, 1998; McLoughlin, 2001), and there is evidence of dispersal events between South America and Africa even much later, during the Eocene, *i.e.* Malpighiaceae (Anderson, 1990). Ocean drilling and sonar investigations in the south Atlantic have demonstrated that the Rio Grande Rise and the Walvis Ridge (on the coasts of



**Figure 17.** Geographical and temporal distribution of sites containing Lactoridaceae.

Brazil and Africa, respectively) may have been emergent until the Oligocene, reducing the distance between these continents (Parrish, 1993; Morley, 2000). Migration of Lactoridaceae in the Cretaceous through the Atlantic Ocean appears to be likely. This is also supported by the fact that the Colorado Basin (with the oldest South American records of Lactoridaceae) had a similar palaeolatitudinal position during the Cretaceous to that of the Orange and Eastern Cape Basins (with the oldest records of the family) in South Africa (*c.* 40°S). We infer that the African–South American connection may have been a probable route for dispersal.

The second option, suggesting a migration via Antarctica, is sustained by previous data (Parrish, 1987; Drinnan & Crane, 1990; Axelrod, Kalin Arroyo & Raven, 1991; Vizcaino *et al.*, 1998). A continuous corridor between South America and Antarctica would have existed during the Late Cretaceous and Palaeogene, with an almost complete floristic continuity in this region (Stuessy & Taylor, 1995). The record of Lactoridaceae in the Maastrichtian of the Antarctic

Peninsula and the presence of suitable forest habitats, somewhat comparable with those in which *Lactoris* lives today, by the latest Cretaceous–Palaeogene in southernmost South America would sustain the Antarctic migration route.

The third alternative, which proposes a migration from North to South America, is also possible. A connection between these two landmasses in the Late Cretaceous (through the Caribbean Plate, the Aves Ridge, and the Greater Antilles) is supported by geological and palaeontological evidence (Parrish, 1987; Pitman *et al.*, 1993). A corridor for the migration of hadrosaurs, ceratopsians, and teiid lizards into South America was required by the Late Cretaceous (Casamiquela, 1964; Bonaparte, 1984a, b, 1986), all with evidence of previous evolution in North America (Bonaparte, 1986).

At present, it is not known how Lactoridaceae arrived in southern South America, and the three connections seem to be viable conduits for dispersal. Moreover, the family may have used more than one route, perhaps at different times. The lack of fossils of

Lactoridaceae in northern and central South America indicates that the North American route may have been less probable than both the African and Antarctic connections.

Another interesting point to analyse is the route followed by the family to its present distribution in an oceanic island. This new fossil find in the Miocene of Patagonia supports a direct migration from the American continent to the island. This dispersal process would have included at least two steps: the first related to the migration of Lactoridaceae within the South American continent towards the Pacific coast, and the second linked to its shift towards Masatierra Island. The first step must have occurred before the Andean maximum uplift (middle–late Miocene), which formed a physical barrier which was unlikely to be passed and which would have prevented later migrations. The Miocene was a period of great geological, climatic, and vegetational changes in South America (Simpson, 1983; Stuessy & Taylor, 1995; Blisniuk *et al.*, 2005). The progressive elevation of the Andean Cordillera, the establishment of the Malvinas cold current, and the development of the Antarctic ice sheet led to the progressive aridity of eastern Patagonia and the shift of forests to the west. Lactoridaceae would have followed a similar migration pattern towards the Pacific coast of South America.

The second migration stage must have been a modern process occurring within the last 4 Myr, representing the age of Masatierra Island, the oldest of the Juan Fernández Archipelago. Potassium–argon dating of basalts from Masatierra Island provides ages of  $3.79 \pm 0.20$  and  $4.23 \pm 0.16$  Myr (Stuessy *et al.*, 1984). Different studies the origin and evolution of island floras have shown that they were derived from chance immigrants that reached the islands by long-distance dispersal and became established. Prevailing wind, distance from continental source areas, ocean current patterns, and bird migration routes would have determined their final floristic composition. The particular characters of the habitats would have determined what species could succeed after arrival and establishment (Mueller-Dombois *et al.*, 1998). Masatierra Island has been colonized for a long period, and its flora has strong American affinities. At about 2 Mya, during the Pleistocene, there was a marked drop in sea-level, reducing the marine barrier between the island and continental South America, which could have helped plant migrations. Some plants, such as those with small seeds, may have been transported to remote islands on the feet of marsh and seashore birds (Johow, 1896). They possess no other means of dispersal to adequately account for their distribution. This means of dispersal may also have been useful for Lactoridaceae.

The present results not only expand the known fossil range of the family to the Miocene, but also help to elucidate the biogeography of this exciting plant family through time. Further fossil discoveries in an accurate stratigraphical framework would surely test and extend our current approach.

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