



# Island evolutionary biogeography: analysis of the weevils (Coleoptera: Curculionidae) of the Falkland Islands (Islas Malvinas)

Juan J. Morrone\*

Museo de Zoología 'Alfonso L. Herrera',  
Departamento de Biología Evolutiva, Facultad  
de Ciencias, Universidad Nacional Autónoma  
de México (UNAM), Apartado Postal 70-399,  
04510 Mexico D.F., Mexico

## ABSTRACT

**Aim** I analysed distributional and phylogenetic information on weevils (Coleoptera: Curculionidae) from the Falklands, and integrated it with molecular, palaeontological and geological information to infer a geobiotic scenario.

**Location** Falkland Islands (Islas Malvinas).

**Methods** The panbiogeographical analysis was based on data on 23 Falkland species and their related taxa from southern South America. For the cladistic biogeographical analysis I analysed six weevil taxa for which phylogenetic hypotheses are available (the generic groups *Cylydrorhinus*, *Strangaliodes* and *Falklandius*, and the genera *Antarctobius*, *Germaniellus* and *Puranius*). Results from this analysis were compared with previous regionalizations. Cenocrons (sets of taxa that share the same biogeographical history) were identified by considering temporal information provided by fossils and molecular clocks. Finally, a geobiotic scenario was proposed by integrating the available information.

**Results** Six generalized tracks were detected: Maule–Valdivian forests, Magellanic forest, Magellanic moorland, Falkland Islands, Magellanic forest–Magellanic moorland, and Magellanic forest–Falkland Islands. A node was identified in the Magellanic forest, based on the overlap of two generalized tracks. A single general area cladogram was obtained, implying the following sequence: (Magellanic moorland (Maule–Valdivian forests (Magellanic forest, Falkland Islands))). The Falklands are classified here as a biogeographical province in the Austral realm, Andean region and Subantarctic subregion. Falkland weevils seem to belong to a single Subantarctic cenocron. The sequence of events deduced implies the following steps: development of the Subantarctic biota in southern South America, arrival of the Falkland crustal block from South Africa in the Early Cretaceous, geodispersal of the Subantarctic cenocron from southern South America to the Falklands during the Early Oligocene, vicariance of the Magellanic moorland, vicariance of the Maule–Valdivian forests, and final vicariance between the Magellanic forest and the Falkland Islands.

**Main conclusions** The biotic components identified support the connection of the Falkland weevils with the Magellanic forest. Falkland weevils belong to a single cenocron, dated to at least the Early Oligocene, when geodispersal from southern South America may have occurred. An older African cenocron may have been replaced completely by the Subantarctic one when the proto-Falklands made contact with the Patagonian continental shelf. A geobiotic scenario implying vicariance events related to sea-level variations could explain the distributional patterns analysed herein.

## Keywords

Cenocrons, cladistic biogeography, evolutionary biogeography, molecular clocks, panbiogeography, weevils.

\*Correspondence: Juan J. Morrone, Museo de Zoología 'Alfonso L. Herrera', Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Apartado Postal 70-399, 04510 Mexico D.F., Mexico.  
E-mail: juanmorrone2001@yahoo.com.mx

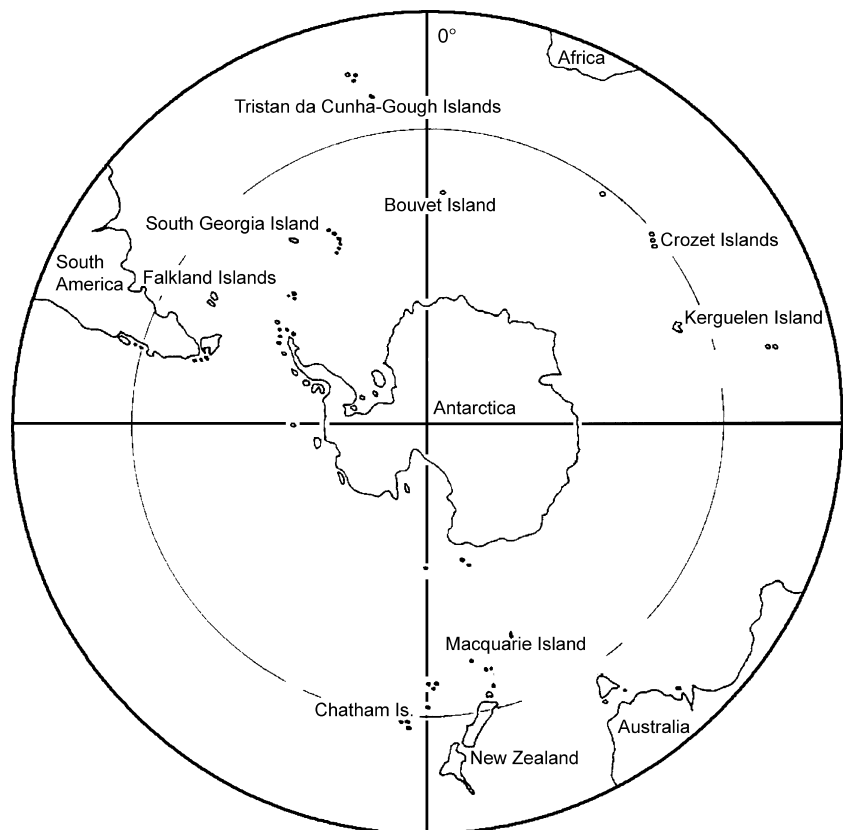
## INTRODUCTION

The Falkland Islands (Islas Malvinas) constitute a large archipelago, of *c.* 12,000 km<sup>2</sup>, comprising two main islands (West Falkland, or Gran Malvina, and East Falkland, or Soledad) and over 780 smaller islets. The natural vegetation is oceanic heath (Moore, 1968), although there is evidence of podocarp-type forests in the pre-Late Tertiary (Birnie & Roberts, 1986). These Subantarctic islands are situated in the South Atlantic Ocean, 520 km east of the Strait of Magellan, stretching from 51° to 52°55' S (Fig. 1). The Falkland Islands are interesting from a biogeographical viewpoint. They are particularly rich compared with other Subantarctic islands (Gressitt, 1970; Papadopoulou *et al.*, 2009), they harbour a high number of endemic species (Ringuelet, 1955; Robinson, 1984; McDowall, 2005; Morrone & Posadas, 2005), they exhibit biotic connections with other Subantarctic areas (Morrone, 1992a), and they have been considered as a relevant area for biodiversity conservation (Oldfield & Sheppard, 1997; Posadas *et al.*, 2000).

Evolutionary biogeography integrates distributional, phylogenetic, molecular and palaeontological data to discover biogeographical patterns and assess the historical changes that have shaped them (Morrone, 2009). It follows five steps, each corresponding to particular questions, methods and techniques. Panbiogeography and methods for identifying areas of endemism are used to identify biotic components, which are the basic units of evolutionary biogeography. Cladistic

biogeography uses phylogenetic data to test the historical relationships among these biotic components. Based on the results of the panbiogeographical and cladistic biogeographical analyses, a regionalization or biogeographical classification is achieved. Intraspecific phylogeography, molecular clocks and fossils may be incorporated to help identify the various cenocrons (sets of taxa that share the same biogeographical history, constituting identifiable subsets within a biotic component by their common biotic origin and evolutionary history) that become integrated in a biotic component. Finally, the geological and biological knowledge available can be integrated to construct a geobiotic scenario that may help explain the way in which the biotic components analysed evolved. This approach is especially suitable for analysing biotic evolution on islands and may play a relevant role in modern island biogeography (Whittaker & Fernández-Palacios, 2007).

Weevils (Coleoptera: Curculionidae) are well suited as study species for an evolutionary biogeographical analysis of the Falkland Islands. They are fairly well known (Morrone, 2002; Posadas, 2002; Morrone & Posadas, 2005), phylogenetic hypotheses are available (Morrone, 1993a, 1994a,b; Morrone & Anderson, 1995; Posadas, 2002; Posadas & Morrone, 2004), and a molecular clock has recently been proposed (Papadopoulou *et al.*, 2009). My objective is to integrate the evidence available in order to construct a geobiotic scenario that may explain the diversification of the Falkland weevils.



**Figure 1** Polar view of the Southern Hemisphere, showing the location of the Falklands and other Subantarctic islands.

## MATERIALS AND METHODS

For the identification of biotic components, a panbiogeographical analysis (Craw *et al.*, 1999) was undertaken. Distributional data were obtained from the literature (Morrone, 1992a,b, 1993a,b, 1994a,b,c, 1995, 1996; Morrone & Anderson, 1995; Morrone & Roig-Juñent, 1995; Posadas & Ocampo, 2001; Posadas, 2002, 2008; Posadas & Morrone, 2004). Some species lacking precise data or known from a single locality were not included in the analysis. The panbiogeographical or track analysis basically consists of plotting the distributions of different taxa on maps and then connecting their separate localities with lines called individual tracks. These tracks represent the geographical coordinates of species or supra-specific taxa, and operationally are lines drawn on a map connecting localities according to their geographical proximity. When different individual tracks are superimposed, the resulting summary lines are considered generalized tracks. Generalized tracks indicate the pre-existence of ancestral biotas, which subsequently become fragmented by tectonic and/or climatic changes. If two or more generalized tracks intersect in a given area, they determine a node or composite area (Morrone, 2009).

In order to test the relationships between the biotic components identified in the first step, I undertook a cladistic biogeographical analysis (Humphries & Parenti, 1999; Parenti & Ebach, 2009). Cladistic biogeography uses information on the phylogenetic relationships between the taxa and their geographic distribution to postulate hypotheses on relationships between areas. If several taxa show the same pattern, such congruence is evidence of a common history. A cladistic biogeographical analysis comprises three basic steps: (1) constructing taxon–area cladograms, from the taxonomic cladograms of two or more taxa, by replacing their terminal taxa with the areas they inhabit; (2) obtaining resolved area cladograms from the taxon–area cladograms (when demanded by the method applied); and (3) obtaining a general area cladogram, based on the information contained in the resolved area cladograms. I analysed a total of six genera and generic groups (groups including two or more genera) for which phylogenetic hypotheses are available: *Cylydrorhinus* generic group (Posadas, 2002), *Strangaliodes* generic group (Posadas, 2002), *Antarctobius* (Posadas & Morrone, 2004), *Falklandius* generic group

(Morrone & Anderson, 1995), *Germainiellus* (Morrone, 1993a, 1994b) and *Puranius* (Morrone, 1994a). Taxonomic cladograms and distributional data of the species were used to generate taxon–area cladograms, by replacing the terminal species by the areas of endemism where they occur (Morrone, 2009). Paralogy-free subtrees were derived applying the transparent method, by resolving widespread taxa so that each area is represented once (Ebach *et al.*, 2005). Components from the paralogy-free subtrees were coded in a data matrix (Table 1), which was analysed with NONA 2.0 (Goloboff, 1999) through WINCLADA 1.00.08 (Nixon, 2002), applying multiple tree bisections and reconnections (León Paniagua & Morrone, 2009).

A regionalization consists of a hierarchical system for categorizing geographical areas in terms of their biotas (Escalante, 2009). The results of the track analysis were compared with previous regionalizations of the Subantarctic subregion, based on other taxa (Morrone, 2000, 2006).

Genocrons can be identified by considering temporal information provided by fossils and molecular clocks (Morrone, 2009). For this step of the analysis, I considered fossil information (Birnie & Roberts, 1986; Buckland & Hammond, 1997; Ashworth & Kuschel, 2003) and the molecular clock provided by Papadopoulou *et al.* (2009).

A geobiotic scenario is obtained by integrating biological and non-biological data to help explain the episodes of vicariance/biotic divergence and dispersal/biotic convergence that may have shaped the evolution of the biotic components analysed. This last step of the analysis was undertaken by correlating the sequence of vicariance events from the general area cladogram with the geological and tectonic information available (Codignotto, 1990; Marshall, 1994; Storey *et al.*, 1999; Trewin *et al.*, 2002).

## RESULTS

### Identification of biotic components

Falkland weevils comprise 23 species, 18 (78%) of which are endemic to the islands (Table 2). These 23 species are assigned to 12 genera, classified into four tribes and three subfamilies (Alonso-Zarazaga & Lyal, 1999; Oberprieler *et al.*, 2007). I discuss below their systematic placement and present their individual tracks.

**Table 1** Data matrix for the cladistic biogeographical analysis of Falkland Island weevils and related taxa in South America. Falk, Falklands; Mage, Magellanic forest; Mauv, Maule-Valdivian forests; Moor, Magellanic moorland. Columns (components from the paralogy-free subtrees): 1–2, *Cylydrorhinus* generic group; 3–4, *Strangaliodes* generic group; 5–8, *Antarctobius*; 9–11, *Falklandius* generic group; 12–14, *Germainiellus*; 15–16, *Puranius*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Root	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mauv	1	0	1	1	0	0	0	0	1	1	0	1	1	0	1	1
Mage	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0
Moor	0	0	0	0	1	0	1	1	1	0	0	1	1	1	0	0
Falk	1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1

**Table 2** Weevil species from the Falkland Islands. Falk, Falklands; Mage, Magellanic forest; Mau, Maule forest; Moor, Magellanic moorland; TC, Tristan da Cunha-Gough Islands; Vald, Valdivian forest.

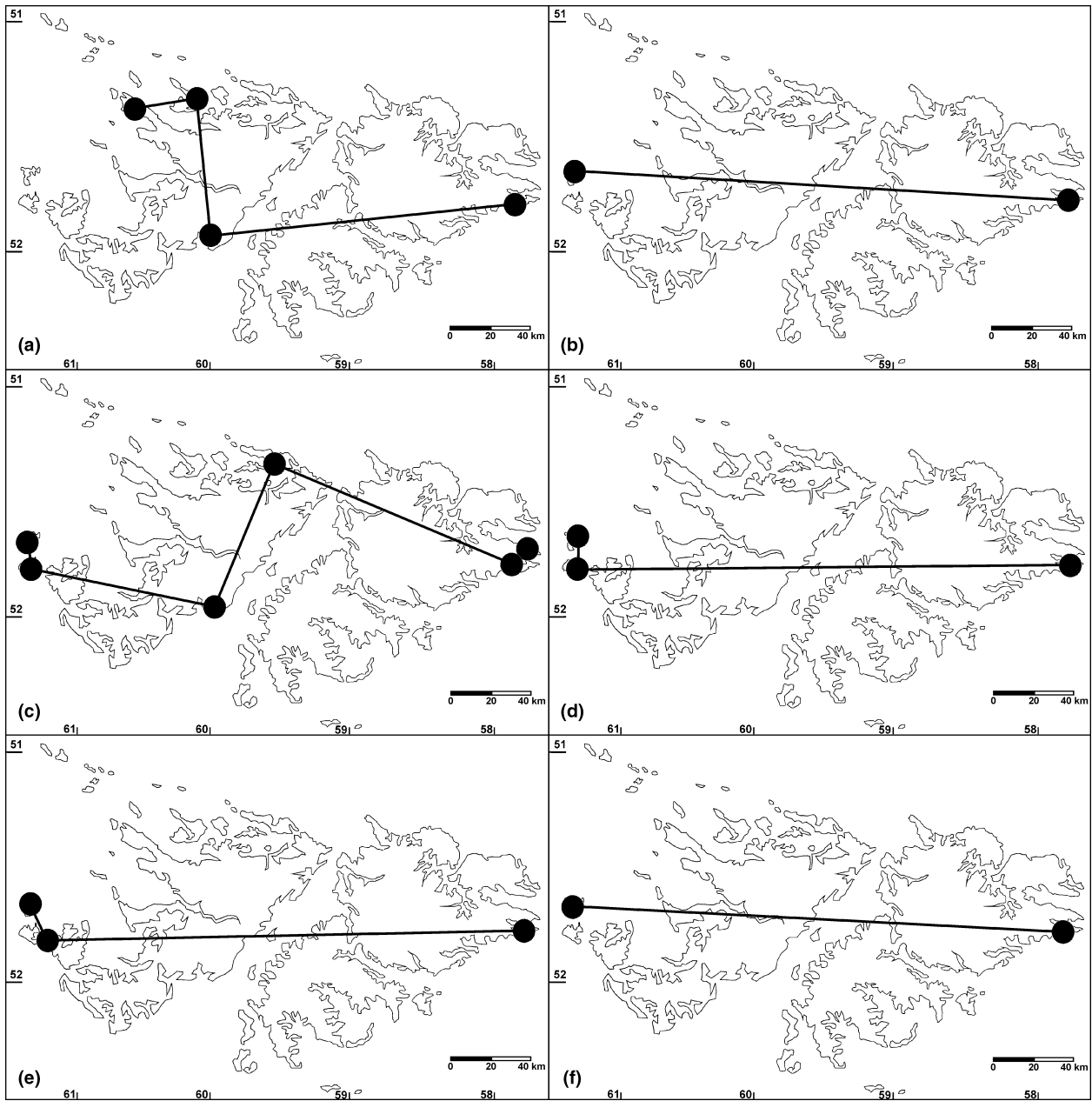
Subfamily	Tribe	Species	Distribution	References
Entiminae	Cylydrorhinini	<i>Caneorhinus biangulatus</i>	Falk	Posadas (2002)
		<i>Cylydrorhinus caudiculatus</i>	Falk, Mage, and Moor	Posadas (2002)
		<i>Cylydrorhinus lemniscatus</i>	Falk	Posadas (2002)
		<i>Morronea brevisrostris</i>	Falk	Posadas & Ocampo (2001)
Entiminae	Tropiphorini	<i>Malvinus compressiventris</i>	Falk	Posadas (2002)
		<i>Malvinus nordenskiöldi</i>	Falk	Posadas (2002)
Cyclominae	Listroderini	<i>Antarctobius abditus</i>	Falk	Morrone (1992b)
		<i>Antarctobius bidentatus</i>	Falk	Morrone (1992b)
		<i>Antarctobius falklandicus</i>	Falk	Morrone (1992b)
		<i>Antarctobius malvinensis</i>	Falk	Posadas & Morrone (2004)
		<i>Antarctobius vulsus</i>	Falk	Morrone (1992b)
		<i>Falklandiellus suffodens</i>	Falk and Mage	Morrone (1995)
		<i>Falklandius antarcticus</i>	Falk, Mage, Mau, Moor, and Vald	Morrone (1992a)
		<i>Falklandius goliath</i>	Falk	Morrone (1992a)
		<i>Falklandius kuscheli</i>	Falk	Morrone (1992a)
		<i>Falklandius turbificatus</i>	Falk	Morrone (1992a)
		<i>Germainiellus salebrosus</i>	Falk	Morrone (1993a)
		<i>Haversiella albolimbata</i>	Falk, Mage, and Moor	Morrone (1994c)
		<i>Lanteriella microphthalmia</i>	Falk	Morrone (1992b)
		<i>Puranius championi</i>	Falk	Morrone (1994a)
		<i>Puranius exculpticollis</i>	Falk	Morrone (1994a)
Cossoninae	Pentarthrini	<i>Puranius scaber</i>	Falk	Morrone (1994a)
		<i>Pentarthrum carmichaeli</i>	Falk and TC	Kuschel (1991)

The tribe Cylydrorhinini (Entiminae) comprises four living genera (*Caneorhinus* Kuschel, *Cylydrorhinus* Guérin, *Machaerophrys* Kuschel and *Morronea* Posadas & Ocampo) and one fossil genus (*Dorotheus* Kuschel, from southern Chile) (Alonso-Zarazaga & Lyal, 1999; Posadas, 2002). The tribe as a whole is distributed in the Andean region, and some species of *Cylydrorhinus* are distributed in the South American Transition Zone (*sensu* Morrone, 2006). *Caneorhinus* has three species (Morrone & Roig-Juñent, 1995; Posadas, 2002), of which one, *Caneorhinus biangulatus* (Champion), is endemic to the Falkland Islands (Fig. 2a). More than 50 species of *Cylydrorhinus* have been described for southern South America (Morrone & Roig-Juñent, 1995), but only two are distributed in the Falklands (Posadas, 2002): *Cylydrorhinus caudiculatus* (Fairmaire), also in southern South America (Fig. 3a), and *C. lemniscatus* (Quoy & Gaimard), endemic to the islands (Fig. 2b). *Morronea* has a single species, *Morronea brevisrostris* Posadas & Ocampo, described for a single locality in the Falklands.

The 115 genera included currently in the tribe Tropiphorini (Entiminae) (see Alonso-Zarazaga & Lyal, 1999) apparently do not constitute a monophyletic taxon. A smaller natural group within it, comprising *Strangaliodes* Schoenherr and related genera, has been proposed by Posadas (2002). The *Strangaliodes* generic group is distributed in several areas of southern South America, New Zealand and Australia (Kuschel, 1991; Posadas, 2002). A single genus from the Falklands, *Malvinus* Kuschel, has two species, both endemic to the islands: *Malvinus compressiventris*

(Enderlein) (Fig. 2c) and *M. nordenskiöldi* (Enderlein) (Fig. 2d).

The tribe Listroderini (Cyclominae) represents the largest weevil higher taxon represented in the Falklands, including the majority of the endemic (and total) species. This tribe includes more than 30 genera, distributed in the Americas (from the United States to Patagonia), Australia, New Zealand and the Tristan da Cunha-Gough Islands (Morrone, 1997; Oberprieler, 2010). Falkland listroderines have been assigned to seven genera: *Antarctobius* Fairmaire, *Falklandiellus* Kuschel, *Falklandius* Enderlein, *Germainiellus* Morrone, *Haversiella* Schweiger, *Lanteriella* Morrone and *Puranius* Germain (Morrone & Roig-Juñent, 1995). *Antarctobius* has 10 species (Morrone, 1992b; Posadas & Morrone, 2004), five of them endemic to the Falkland Islands: *Antarctobius abditus* (Enderlein), *A. bidentatus* (Champion), *A. falklandicus* (Enderlein) (Fig. 2e), *A. malvinensis* Posadas & Morrone and *A. vulsus* (Enderlein) (Fig. 2f). The single species of *Falklandiellus*, *Falklandiellus suffodens* (Enderlein), is distributed in the Falklands and the Magellanic forest (Morrone, 1995; Posadas, 2002) (Fig. 3b). *Falklandius* has six species (Morrone, 1992a; Morrone & Anderson, 1995): *Falklandius antarcticus* is widespread in the Maule, Valdivian and Magellanic forests and the Falklands (Fig. 3c), and *F. goliath* Morrone, *F. kuscheli* Morrone and *F. turbificatus* Enderlein (Fig. 4a) are endemic to the Falklands. *Germainiellus* has 12 species (Morrone, 1993a, 1994b), of which only *Germainiellus salebrosus* (Enderlein) is endemic to the Falklands (Fig. 4b). The single species of *Haversiella*, *Haversiella albolimbata* (Champion), is distributed in the



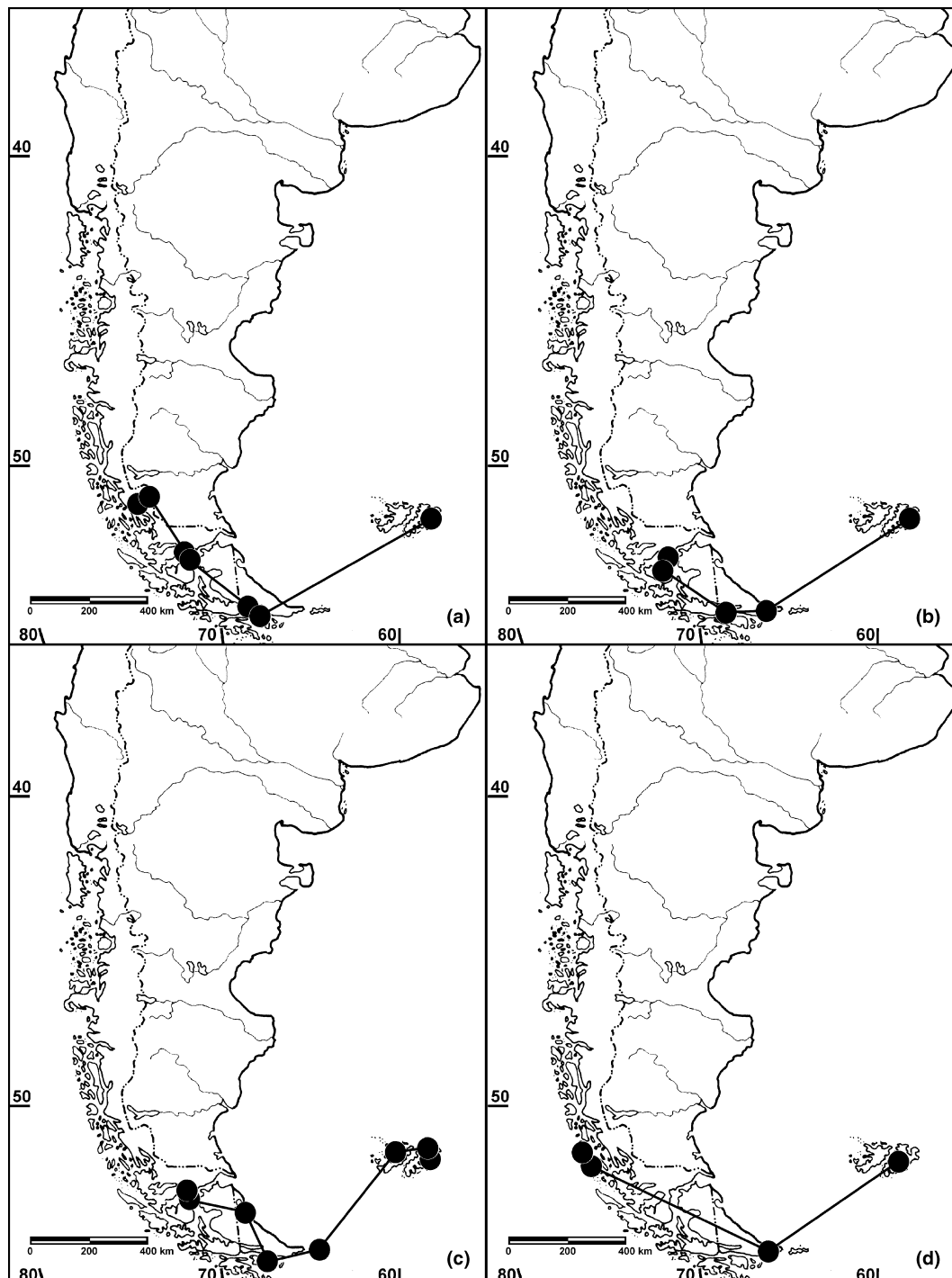
**Figure 2** Individual tracks of six weevil species endemic to the Falkland Islands. (a) *Caneorhinus biangulatus*; (b) *Cydrorhinus lemniscatus*; (c) *Malvinus compressiventris*; (d) *Malvinus nordeskoeldi*; (e) *Antarctobius falklandicus*; (f) *Antarctobius vulsus*.

Falklands, Magellanic forest and Magellanic moorland (Morrone, 1994c; Posadas, 2002) (Fig. 3d). The single species of *Lanteriella*, *Lanteriella microphtalma* Morrone, is endemic to the Falklands (Morrone, 1992a). *Puranius* has 20 species (Morrone, 1994a), three of which are endemic to the Falkland Islands: *Puranius championi* (Kuschel) (Fig. 4c), *P. exsculpticollis* (Enderlein) and *P. scaber* (Enderlein) (Fig. 4d).

The tribe Pentarthrini (Cossoninae) comprises 50 genera (Alonso-Zarazaga & Lyal, 1999). *Pentarthrum* occurs across a broad range in the Americas, Japan, Africa, New Guinea, New Caledonia, Hawaii and other areas. The only species found in

the Falklands, *Pentarthrum carmichaeli* C. O. Waterhouse, has been reported by Kuschel (1991) and Buckland & Hammond (1997), but only one specific locality (Beauchene Island) has been provided. This species is found in *Nothofagus* (Nothofagaceae) driftwood from southern South America, and has been also found in the Tristan da Cunha-Gough Islands (Thompson, 1989; Kuschel, 1991).

Individual tracks of the species from the Falkland Islands and of the species belonging to the same genera or generic groups were compared. Based on their overlap, six generalized tracks were detected (Fig. 5), as follows.

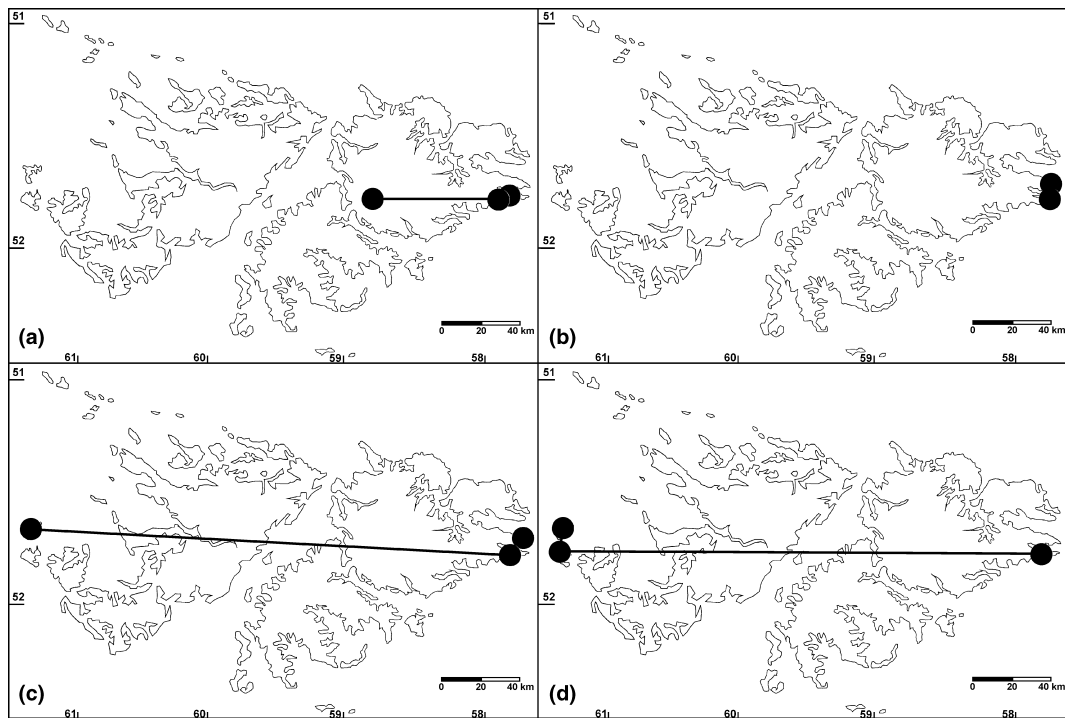


**Figure 3** Individual tracks of four weevil species distributed in the Falkland Islands and southern South America. (a) *Cyldrorhinus caudiculatus*; (b) *Falklandiellus suffodens*; (c) *Falklandius antarcticus*; (d) *Haversiella albolimbata*.

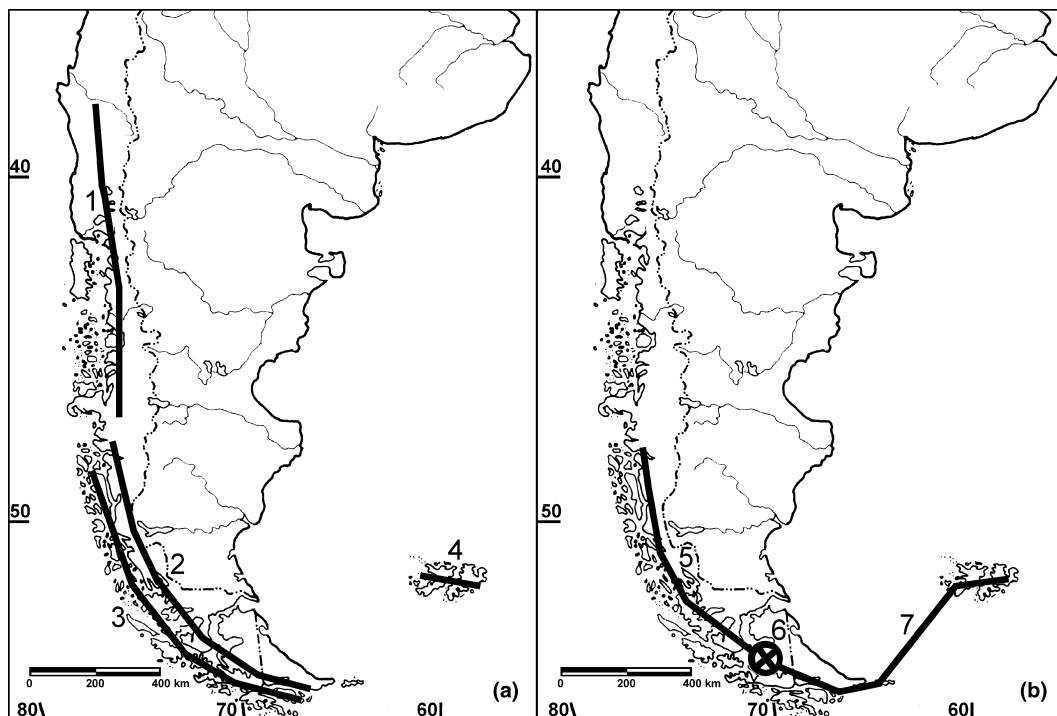
1. Maule–Valdivian forests – supported by *Chileudius varians*, *Hybreoleptops tuberculifer*, *Megalometis spinifer* and *Strangaliodes mutuarius* (Tropiphorini), and *Falklandius peckorum* and *Puranius fasciculiger* (Listroderini). The Maule Forest province comprises southern Chile and Argentina between latitudes 36° and 39° S, and the Valdivian Forest

province comprises southern Chile and Argentina, south of the Maule province, reaching latitude 47° S (Morrone, 2006).

2. Magellanic forest – supported by *Caneorhinus lineatus* and *C. tessellatus* (Cyldrorhinini), and *Antarctobius lacunosus*, *Falklandiopsis magellanica* and *Telurus dissimilis* (Listroderini).



**Figure 4** Individual tracks of four weevil species endemic to the Falkland Islands. (a) *Falklandius turbificatus*; (b) *Germainiellus salebrosus*; (c) *Puranius championi*; (d) *Puranius scaber*.



**Figure 5** Generalized tracks and node obtained. (a) 1, Maule-Valdivian forests generalized track; 2, Magellanic forest generalized track; 3, Magellanic moorland generalized track; 4, Falkland Islands generalized track; (b) 5, Magellanic forest-Magellanic moorland generalized track; 6, node; 7, Magellanic forest-Falkland Islands generalized track.

The Magellanic Forest province comprises southern Chile, from latitude 47° south to Cape Horn, and southern Argentina in small areas of western Santa Cruz and Tierra del Fuego (Morrone, 2006).

3. Magellanic moorland – supported by *Antarctobius rugirostris* and *A. yefacel* (Listroderini). The Magellanic moorland province comprises southern Chile and Argentina, from the Golfo de Penas (latitude 48° S) to Cape Horn, bordered to the west by the Magellanic Forest province (Morrone, 2006).

4. Falkland Islands – supported by *Caneorhinus biangulatus*, *Cylydrorhinus caudiculatus*, *Cylydrorhinus lemniscatus* and *Morronea brevirostris* (Cylydrorhinini), *Malvinus compressiventris* and *M. nordenskiöldi* (Tropiphorini), and *Antarctobius abditus*, *A. bidentatus*, *A. falklandicus*, *A. malvinensis*, *A. vulsus*, *Falklandius goliath*, *F. kuscheli*, *F. turbificatus*, *Lanteriella microphthalmia*, *Puranius championi*, *P. exsculpticollis* and *P. scaber* (Listroderini).

5. Magellanic forest–Magellanic moorland – supported by *Antarctobius germaini*, *A. hyadesii* and *Telurus caudiculatus* (Listroderini).

6. Magellanic forest–Falkland Islands – supported by *Falklandiellus suffodens* and *Falklandius antarcticus* (Listroderini).

A node (Fig. 5b) was identified in the Magellanic forest, based on the overlap of two generalized tracks: Magellanic

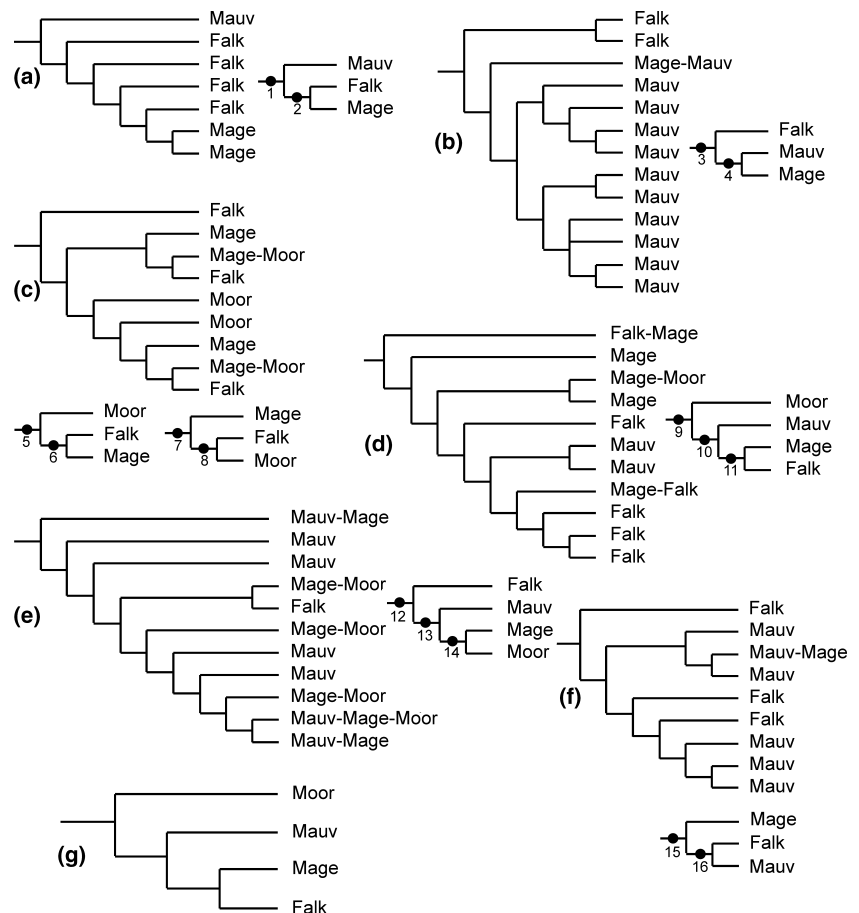
forest–Magellanic moorland and Magellanic forest–Falkland Islands.

### Relationships of the biotic components

Six taxon–area cladograms and seven paralogy-free subtrees derived from them were obtained for the *Cylydrorhinus* generic group (Fig. 6a), *Strangaliodes* generic group (Fig. 6b), *Antarctobius* (Fig. 6c), *Falklandius* generic group (Fig. 6d), *Germainiellus* (Fig. 6e) and *Puranius* (Fig. 6f). The parsimony analysis of the data matrix (Table 1) led to a single general area cladogram (Fig. 6g), with 21 steps, a consistency index of 0.76 and a retention index of 0.44. The sequence in this general area cladogram allows identification of the following sequence of vicariance events: (Magellanic moorland (Maule–Valdivian forests (Magellanic forest, Falkland Islands))).

### Regionalization

The Falkland Islands have been classified according to the following regionalization: Austral realm (Engler, 1899; Moreira-Muñoz, 2007), Andean region (Shannon, 1927) and Subantarctic subregion (Cabrera, 1951). Within the latter, they have been treated as a biogeographical province (Morrone, 2000, 2006).



**Figure 6** Taxon–area cladograms and the paralogy-free subtrees derived from them. (a) *Cylydrorhinus* generic group; (b) *Strangaliodes* generic group; (c) *Antarctobius*; (d) *Falklandius* generic group; (e) *Germainiellus*; (f) *Puranius*; (g) General area cladogram. Falk, Falklands; Mage, Magellanic forest; Mauv, Maule–Valdivian forests; Moor, Magellanic moorland.

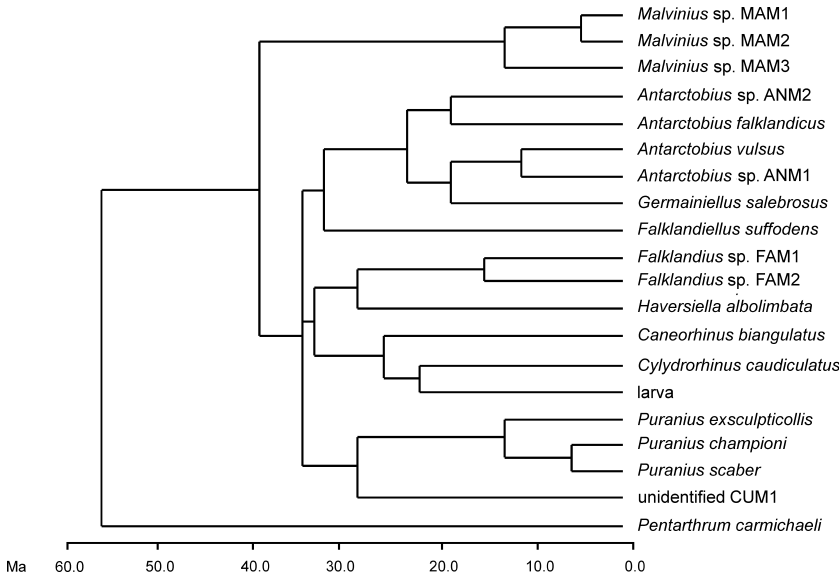


Within the Falkland Islands, no further divisions have been proposed. In this analysis, weevil distribution patterns do not permit recognition of smaller biogeographical units within the islands. If South Georgia Island is included in the Falkland Islands province, however, it may deserve recognition as a distinct district.

**Identification of cenocrons**

The analysis of the weevil taxa from the Falklands seems to indicate that they all belong to a single cenocron. A possible

exception is *Pentarthrum carmichaeli*, which may have dispersed recently to the islands in association with *Nothofagus* driftwood. Molecular clock estimates (Papadopoulou *et al.*, 2009) suggest that separation of species endemic to the Falklands from their sister species pre-dated the Oligocene (Fig. 7). Minimum ages of the Falkland weevil lineages were found to be greater than previously suggested; for example, the basal internal split of the genus *Malvinus*, endemic to the Falklands, has been estimated to be at least  $4.17 \pm 1.9$  Ma (Papadopoulou *et al.*, 2009). This cenocron is clearly Subantarctic, representing an extension of the southern South



**Figure 7** Clock-constrained chronogram of the Falkland weevils (modified from Papadopoulou *et al.*, 2009).



**Figure 8** Geobiotic scenario explaining the biotic evolution of the Falkland biota. (a) Development of the Subantarctic biota in southern South America; (b) arrival of the Falkland Islands crustal block from South Africa; (c) geodispersal from the Subantarctic biota from southern South America to the Falklands; (d) vicariance of the Magellanic moorland; (e) vicariance of the Maule–Valdivian forests; (f) final vicariance between the Magellanic forest and the Falkland Islands.

American biota. Its geodispersal to the Falklands might have occurred during the Early Oligocene (Birnie & Roberts, 1986; Morrone & Posadas, 2005).

### Construction of a geobiotic scenario

The sequence of events deduced from the general area cladogram and the geological, tectonic and palaeontological information available (Birnie & Roberts, 1986; Codignotto, 1990; Marshall, 1994; Buckland & Hammond, 1997; Storey *et al.*, 1999; Trewin *et al.*, 2002; Ashworth & Kuschel, 2003) imply the following steps (Fig. 8).

1. Development of the Subantarctic biota in southern South America.
2. Arrival of the Falkland Islands crustal block from South Africa in the Early Cretaceous.
3. Geodispersal of the Subantarctic cenocron from southern South America to the Falklands during the Early Oligocene.
4. Vicariance of the Magellanic moorland.
5. Vicariance of the Maule–Valdivian forests.
6. Final vicariance between the Magellanic forest and the Falkland Islands.

This final step is the most relevant for this analysis. Geological evidence suggests that several glaciations occurred during Tertiary and Quaternary times in the Southern Hemisphere, and during these episodes the geographical isolation of the Falklands was broken. The coastline during the final Pleistocene glaciation was located between the 100- and 150-m present-day bathymetric curves (Codignotto, 1990), so most of the continental shelf of southern South America (where the Falkland Islands are situated) was an emerged land mass during glaciations. Episodes of sea-level variations induced by glacial-eustatic agents may have caused the vicariance between the Magellanic forest and the Falkland Islands.

### DISCUSSION

The biotic components that were identified support the Subantarctic connection of the Falkland weevils, as has been previously noted for insects (Enderlein, 1907; Champion, 1918; Schweiger, 1959; Kuschel, 1960; Morrone, 1998), spiders (Grismado & Platnick, 2008), mites (Colloff, 2009), several other invertebrates (Ringuelet, 1955; McDowall, 2005) and birds (Bulgarella *et al.*, 2010). Previous authors have noted particularly the close relationships between the weevil faunas of the Falkland Islands and of the Magellanic forest (Schweiger, 1959; Kuschel, 1960, 1971; Morrone, 1998; Anderson & Fuller, 2005). Although older African biotic connections have been occasionally noted, for example for amphipods (Barnard & Barnard, 1983), isopods (Green, 1974) and oligochaetes (Brinkhurst & Jamieson, 1971), they have been dismissed because they are poorly defined or in need of phylogenetic corroboration (McDowall, 2005). The Falkland biota seems to be related to that of the rest of the Subantarctic subregion, in southern South America.

The general area cladogram obtained is similar to a previous one (Morrone, 1993a), based on three of the taxa analysed herein (*Antarctobius*, *Falklandius* and *Gernainiellus*). Two other cladistic biogeographical analyses (Morrone *et al.*, 1994; Posadas & Morrone, 2003), however, have indicated a close relationship between the Falkland Islands and the Magellanic forest–Magellanic moorland. It is possible that inclusion of taxa from other cenocrons, for example the *Anthonomus ornatus* species group (Morrone *et al.*, 1994) or *Aegorhinus* and *Rhyephenes* (Posadas & Morrone, 2003), have influenced these results. Another cladistic biogeographical analysis (Soares & Carvalho, 2005) also indicated an early vicariance of the Magellanic moorland.

The general distributional uniformity of the weevil species from the Falkland Islands biogeographical province, previously noted by Voisin (1987), does not permit recognition of further biogeographical units within the province. Plant species show the same uniformity (Moore, 1968; Broughton & McAdam, 2005). South Georgia Island has several species in common with the Falklands (Darlington, 1970; Steel, 1970; Ernsting *et al.*, 1995; Pugh, 2004) and may be recognized as a distinct district within the Falkland Islands province, based on the presence of several endemic taxa (Gressitt, 1970; Robinson, 1984; Erséus & Grimm, 2002).

Falkland weevils seem to belong to a single cenocron, dating to at least the Early Oligocene, when geodispersal from southern South America may have occurred (see evidence for forest habitats in the Falkland Islands by Birnie & Roberts, 1986). *Pentarthrum carmichaeli* is the only possible exception; its widespread distribution on other Subantarctic islands is shared with *Kenodactylus audouini* Guérin-Ménéville (Coleoptera: Carabidae) (Roig-Juñent & Domínguez, 2001), and it may belong to a more recent cenocron. An older African cenocron may have been replaced completely (or almost completely) by the Subantarctic one when the proto-Falklands made contact with the Patagonian continental shelf (McDowall, 2005). Analyses from other taxa also suggest the existence of different cenocrons in the Falklands (Starý & Block, 1996).

Palaeogeographical investigations established that at 200 Ma the shelf region that makes up the Falkland Islands was part of eastern South Africa. It moved from this position with the break-up of Gondwanaland (Marshall, 1994). The Falkland Islands crustal block was carried westwards with the South American plate, to which it has been linked since before the break-up of Africa and South America some 130 Ma (Storey *et al.*, 1999; Trewin *et al.*, 2002). None of the taxa analysed to date appear to reflect these ancient geological affinities with Africa, whereas relationships with South American taxa are strongly corroborated by phylogenetic and panbiogeographical analyses (Heads, 1999; McDowall, 2005; Morrone & Posadas, 2005). Sea-level changes during the Tertiary and, in particular, the most recent glacial cycles might have resulted in temporary land connections between the Falklands and southern South America. This would require a drop of sea level of only 100–150 m. Periglacial conditions might have been severe enough to cause the local extinction of most terrestrial species,

and it has been postulated that Falklands insects might have colonized the islands during the last 15–10 kyr (Buckland & Hammond, 1997). The analysis of Papadopoulou *et al.* (2009), however, has shown that the separation of the Falkland endemics and their sister species pre-dated the Pleistocene. Furthermore, microfossils have shown that the Falklands harboured podocarp-type forests with some *Nothofagus* and tree ferns in the Early Oligocene (Birnie & Roberts, 1986), and listroderine weevils are known from Pliocene forests in Antarctica (Ashworth & Kuschel, 2003).

A geobiotic scenario implying vicariance events related to sea-level variations, induced by glacial-eustatic agents, could explain the distributional patterns analysed in this paper. Species endemic to the Falklands do not constitute monophyletic clades, but have their sister groups in continental areas of southern South America (Posadas & Morrone, 2004). Data on the age of the Falkland weevil taxa suggest that Pleistocene glaciations did not extirpate the existing biota and that ancient lineages persisted *in situ*, possibly for > 10 Myr (Papadopoulou *et al.*, 2009). There is fossil evidence showing that the Falkland forests originally inhabited by these weevils date back at least to the Early Oligocene (Birnie & Roberts, 1986).

Island biogeography remains a dynamic research programme, which feeds ideas, theories and models to ecology and evolutionary biology. Island evolutionary biogeography has classically analysed species as standard units. New insights in evolutionary approaches have contributed in recent decades to the construction of scenarios for evolutionary and distributional changes on a lineage-by-lineage basis (Whittaker & Fernández-Palacios, 2007). It is to be hoped that this integrative analysis, as adopted here, can contribute to an emerging model of evolutionary biogeography on islands.

## ACKNOWLEDGEMENTS

I thank Michael Baehr, Amparo Echeverry, Tania Escalante, Michael Heads, Analía Lanteri and Paula Posadas for useful comments on the manuscript.

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## BIOSKETCH

**Juan J. Morrone** is a professor of biogeography, systematics and comparative biology at the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM). His main interests are in phylogenetic systematics and evolutionary biogeography.

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Editor: Malte Ebach