CHAPTER 1

General Introduction, Rationale and Key Questions

Mayr (1942) introduced the 'biological species concept' namely that "*species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups*". Reproductive isolation is thus the *sine qua non* of a good species. The reproductive barriers that separate members of different species are divided into two groups, namely 'prezygotic isolating factors' (arising from mate discrimination, different habitat preferences, pollination by different insects, amongst others) and 'postzygotic isolating factors' (due to hybrid inviability and/or sterility). It is argued that reproductive isolation usually evolves in allopatry when different populations of the same species are isolated from each other by geographic barriers, and that allopatric speciation is the primary mode of speciation in nature (Futuyma & Mayer, 1980; Mayr, 1963; Coyne & Orr, 2004). Together with selection (Darwin, 1859) and genetic drift (Mayr, 1954), reproductive isolation creates and expands the morphological differences between closely related species (Mayr, 1954). Genetic drift is far more likely in island or peripheral populations founded by a few individuals and may allow rapid evolution to new fitness peaks, permitting the evolution of reproductive isolation between ancestral and founder populations (Mayr, 1954; Provine, 1989). Dobzhansky (1937) also proposed that when populations have diverged genetically to the extent that the offspring of within-population matings are more fit than hybrid offspring, selection favours an increase in non-random mating due to a preference for similar partners. This assortative mating then increases reproductive isolation by reducing the exchange of genes between the original populations, a process termed reinforcement. Support for reinforcement has been found in nature in flycatchers (Saetre et al., 1997).

It is also believed that speciation can occur between populations that occupy the same area, a process called sympatric speciation. Rice (1984) presented a model in which reproductive isolation and thus sympatric speciation can occur due to disruptive selection on habitat preference. Reproductive isolation has also been shown to occur by mate preference as seen in sticklebacks in Canadian lakes (Boughman, 2001). Dieckmann & Doebeli (1999) presented a model that shows that assortative mating due to differences in preference for a certain trait within a large species may split the species in two. Doebeli & Dieckmann (2003) provides another model for sympatric speciation where the outer ends of a species that occurs

over an environmental gradient adapt, over time, through internal competition to those circumstances and diverge from each other to form different species as selection in each part of the original species favours a different trait. Mutations in as little as one gene can cause reproductive isolation in some species as is seen in prezygotic isolation in snails where the direction in coiling can be changed by a single mutation, making copulation impossible (Orr, 1991). On the other hand it has been shown that at least 150 genes are responsible for inviability in hybrids between two chromosomal races of the grasshopper *Podisma pedestris* (Barton & Hewitt, 1981).

Another view on speciation is the phylogenetic species concept (Cracraft, 1983). Here a species is identified as an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent. Nixon & Wheeler (1990), identify a species as the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals. Baum and Donoghue, (1995), on the other hand, identify a species as a basal group of organisms, whose genes all coalesce more recently with each other than with those of any organisms outside the group.

As isolated species such as those on oceanic islands often display more disparate morphological differences than related species on continents and as speciation on isolated islands often occurs very rapidly, different theories have been developed to explain how speciation has come about on these islands. One theory proposes that as an island is colonized by only a few founder individuals, they could experience large changes in their allele frequencies from random genetic drift. This may then explain rapid changes in morphology leading to reproductive isolation (Mayr, 1963; Carson & Templeton, 1984). Another theory proposes adaptive radiation. This is when a recent ancestor undergoes speciation and phenotypic adaptation which gives rise to an array of species exhibiting different morphological and physiological traits with which they can exploit a range of divergent environments (Barton & Charlesworth, 1984).

The Prince Edward Island Archipelago (PEIA) consists of two volcanic islands, Marion Island (MI) and Prince Edward Island (PEI), that lie approximately 1770 km south-east of Port Elizabeth, South Africa, the closest point to any continent (Hänel & Chown, 1999a). Together with Crozet, Kerguelen, Heard and MacDonald Islands, these islands form the South Indian Ocean Province (SIP). Marion Island (MI), the larger (290 km^2) and more south-westerly (46 54' S; 37 45' E) of the two islands is separated from the smaller (42 km^2) PEI (46 38' S; 37 57' E) by 19 km. While MI rises to a height of 1,230 m above sea level

(a.s.l.), PEI has a maximum elevation of 672 m (Verwoerd, 1971). Both islands are estimated to be approximately 500,000 years old (McDougall *et al*., 2001; Boelhouwers, 2008). The geographic isolation of the PEIA along with the strict control on human activities on these islands (PEIMPWG, 1996; Davies *et al*., 2007) make them an ideal natural laboratory that has been exploited for scientific research since the annexation of the islands by South Africa in 1948 (See Hänel & Chown 1999b and Chown & Froneman 2008 for more information).

The PEIA is especially well-situated to study climate change. The sea surface temperature around MI has increased by 1.4° C between 1949 and 1999 (Mélice *et al*., 2003) and the air temperature has increased by 1.2° C over the same period (Smith, 2002; le Roux & McGeoch, 2008). Daily maximum and minimum temperatures have also increased at a similar rate as mean temperature increases (le Roux & McGeoch, 2008). It has been suggested that MI may be a true sentinel for future changes in climate (Bergstorm & Chown, 1999). The small size of the PEIA provides an opportunity to study the effects of climate change on terrestrial and oceanic life. It has been noted, for instance, that the contribution of Antarctic zooplankton species in the region of the PEIA has decreased by some 20 % while the contribution of sub-tropical species has increased from 6 % to 26 % over the past two decades (Pakhomov *et al*., 2001).

Climatic changes also result in changes in interactions between indigenous and invasive species. Bergstorm & Chown (1999) have indicated that warmer climates increase the ease with which invasive alien organisms can become established on the PEIA. Although it was shown that most indigenous species on the PEIA are likely to survive an increase in temperature of several degrees (Slabber, 2005), these temperature increases will favour invasive species that are less tolerant of low temperatures than indigenous species (Slabber *et al*., 2007). Warmer climates will therefore, not only increase the ease with which introduced alien organisms can become established on the PEIA, but will also allow already established invasive species to expand their distributional ranges and to aggravate their effects on local species and ecosystems (Pakhomov & Chown, 2003).

A good example of an interaction between indigenous and invasive species is that between the invasive feral house mouse, *Mus musculus domesticus* (Jansen van Vuuren & Chown, 2007) and the weevils of the *Ectemnorhinus* group of genera (Kuschel & Chown, 1995). *Mus m. domesticus* was introduced to MI by sealers in the early 1800s (Hänel & Chown, 1999a), while PEI has remained mice-free. The introduced *Mus* feed on a variety of plants and invertebrates on MI, and especially on *Ectemnorhinus* weevils (Gleeson and van Rensburg, 1982; Smith *et al*., 2002). The mean volume contribution of weevil adults found in

the guts of mice increased from 7 % in 1979/1980 (Gleeson and van Rensburg, 1982) to 11 % in 1992/1993 (Smith *et al*., 2002). House mice are thus considered to be responsible for the significant change in the populations of *Ectemnorhinus* species on MI, leading to almost an order of magnitude decline in biomass between 1976 and 1996 (Chown *et al*., 2002), and a pronounced difference between population densities on MI and PEI (Crafford and Scholtz, 1987). Mice are also thought to have caused a reduction in the body size of weevil species on MI relative to PEI, due to size-selective mice predation, as the body size frequency distributions of the *Ectemnorhinus* species differ considerably between the two islands (Chown and Smith, 1993).

The group of flightless weevils (Curculionidae: Coleoptera: Hexapoda) belonging to the *Ectemnorhinus* group of genera (Kuschel & Chown, 1995) or the tribe Ectemnorhinini (Alonso-Zarazaga & Lyal, 1999) is restricted to islands of the sub-Antarctic South Indian Ocean Province. This group of weevils comprises six genera and 36 flightless species (Kuschel & Chown, 1995), of which six occur on the Prince Edward Islands Archipelago. Of these six species, four, namely *Ectemnorhinus similis* (Waterhouse, 1885), *E. marioni* (Jeannel, 1940), *Bothrometopus parvulus* (Waterhouse, 1885) and *B. elongatus* (Jeannel, 1953), are endemic to the archipelago, with *B. randi* (Jeannel 1953) also being found on the Crozet archipelago to the east, and *Palirhoeus eatoni* (C.O. Waterhouse 1876) occurring on all SIP islands (Chown & Klok, 2001; Kuschel & Chown, 1995). Although the PEIA species were all described from MI, it has long been accepted that all also occur on PEI (Chown, 1992; Chown, 1994; Chown *et al*., 1998).

The *Ectemnorhinus* group of genera (Kuschel & Chown, 1995) has proven to be a taxonomically difficult group (Brown, 1964; Kuschel, 1970; Dreux & Voisin, 1989; Chown, 1991). Chown (1990) argued that the endemic *E. marioni* and *E. similis* are two morphologically similar, but ecologically distinct species. *Ectemnorhinus marioni* individuals are smaller in body size (3.77 mm – 7.79 mm; median: 5.53 mm) and feed on bryophytes while *E. similis* individuals are larger (4.51 mm – 8.69 mm, median: 6.44 mm) and feed mainly on angiosperms although bryophytes and other cryptogams are incorporated into their diet at the end of the growing season when vascular plant foliage deteriorates (Chown, 1989; Chown and Scholtz, 1989; Chown, 1990). It has been suggested that *E. marioni* and *E. similis*, with their island wide distribution, evolved sympatrically in a manner similar to that proposed by Rice (1984), with reproductive isolation being induced by size-based assortative mating associated with differences in food preference (Chown, 1990; Crafford and Chown, 1991). Endemic *B. parvulus* predominantly occurs in epilithic moss cushions from coastal

rock faces to high altitude fellfield and polar desert. The larvae and adults feed on algae, lichens, and bryophytes (Chown, 1989; 1992). Individuals may occur occasionally on *Azorella selago*, but feed on epiphytic algae and bryophytes, rather than on the plant itself (Chown, 1989; 1992). On both Marion and Prince Edward Islands, *B. parvulus* shows distinct variation in body size, associated both with elevation and habitat type, although differences among the two islands are not pronounced. *Bothrometopus parvulus* individuals are characterised by a compressed and carinate humeral area (Chown, 1992; Chown & Smith, 1993; Chown & Klok, 2003). *Bothrometopus elongatus* is the smallest weevil species present on Marion and Prince Edward Islands and adults are readily distinguished from other species based on the presence of long transberse hairs on the elytra and pronotum. Adults feed on lichen and epilitic moss and are restricted to the central highlands between 300 and 1000 m a.s.l. (Crafford *et al*., 1986; Chown, 1992). The largest weevil species on Marion and Prince Edward Islands, *B. randi*, occurs from sea level up to 1000 m a.s.l. on lichen-covered rocks. Adults and larvae feed on algae and lichen. Adults are distinguished from other species by a distinctive green elytra scale pattern (Crafford *et al*., 1986; Chown, 1992). *Palirhoeus eatoni* feed on marine algae and are restricted to the upper- to supra-littoral zone where they are regularly inundated and exposed to sea spray. Adults are distinguished from other species by the presence of a tarsal claw segment that is longer than the first three tarsal segments (Crafford *et al.*, 1986; Chown, 1992).

Studying the phylogenetics and biogeography of the different species within the *Ectemnorhinus* group of genera (Kuschel & Chown, 1995) will present unique opportunities to investigate the evolutionary history of the group as well as theories underpinning evolution. When comparing the known geological data with the biogeographical data, this will also provide us with insights into the history and colonization of the islands.

Relevance of this study

Until the present study, all studies of the *Ectemnorhinus* group of genera (Kuschel & Chown, 1995) from the PEIA relied primarily on morphology. No studies had been conducted to determine whether the morphological species classifications concur with results from molecular-based studies. It is also important to understand the within- and between-island biogeography of the species in order to maximise the conservation of the *Ectemnorhinus* group of genera. The *Ectemnorhinus* group of genera (Kuschel & Chown, 1995) is a preferred prey species of the invasive feral house mouse (Gleeson and van Rensburg, 1982; Smith *et al.* 2002) and decisions need to be made on how to effectively

protect endemic species from predation by invasive aliens. By protecting the *Ectemnorhinus* weevils from annihilation by invasive predators, the effect of climate change can be studied on these insects that might also provide valuable insights on how climate change may influence other ecosystems in the future. The Prince Edward Islands Management Plan (PEIMPWG, 1996), under which the PEIA is environmentally managed, is currently under revision (Chown *et al*., 2006). However, there is always a critical need to improve this management plan (see de Villiers & Cooper, 2008).

The rationale of this study is thus to improve our knowledge on the species dynamics and biogeography of the *Ectemnorhinus* group of genera (Kuschel & Chown, 1995) in order to make scientifically based informed decisions on how to conserve this unique group of weevil species. The aims of this study were thus to resolve phylogenetic relationships of the *Ectemnorhinus*-group of taxa and to use historic population dynamics in order to elucidate phylogeograpic patterns. This information will serve to guide informed conservation recommendations.

Key research questions

The key research questions that will be addressed in the present study include:

Chapter 2 - **Molecular and morphometric assessment of the taxonomic status of *Ectemnorhinus* weevil species (Coleoptera: Curculionidae, Entiminae) from the sub-Antarctic Prince Edward Islands.**

Key research question:

Q1: What is the current taxonomic status of the *Ectemnorhinus* weevil species occurring on the Prince Edward Islands?

Chapter 3 – **The population dynamics of the *Ectemnorhinus* weevils from the Prince Edward Island Archipelago.**

Key research questions:

Q1: It is possible, with the use of molecular techniques, to distinguish between the different scenarios proposed in Chapter 2, for:

(i) The existence of a single *Ectemnorhinus* species on MI that is best explained by:

a) There were originally two species of *Ectemnorhinus* present on MI but one was lost, possibly through size selective predation by mice (Chown and Smith 1993; Smith et al. 2002) and rapid climatic changes (Smith, 2002).

or

b) The extreme morphological variation observed for *Ectemnorhinus* on MI was wrongly interpreted as indicating the presence of two species.

versus

(ii) two *Ectemnorhinus* species on PEI which were proposed to have arisin due either to:

a) Weevils on PEI having had longer exposure to vascular plants as an additional, more nutritious food source to bryophytes than those on MI, leading to divergence in sympatry according to the model of Rice (1984), resulting in two species: a smaller one with a preference for bryophytes and a larger one with a preference for angiosperms, as suggested by Chown (1990).

or

b) The weevils on PEI and MI diverged from each other allopatrically resulting in a MI *Ectemnorhinus* species and a PEI *Ectemnorhinus* species, with the subsequent colonization of PEI by the MI *Ectemnorhinus* species explaining the presence of two species on PEI.

Q2: How does the genetic history of the *Ectemnorhinus* weevils present on MI compare with the island's geological history?

Chapter 4 – **Cryptic species, phylogenetic complexity and the evolutionary history of the** *Ectemnorhinus*-**group in the sub-Antarctic, including a description of** *Bothrometopus huntleyi n. sp*.

Key research question:

Q1: What is the phylogenetic relationships among species from the genera *Palirhoeus*, *Bothrometopus* and *Ectemnorhinus* based on the material available for the group from Heard Island in the East through to the Prince Edward Islands in the west?

Chapter 5 – **Inter-island dispersal of flightless *Bothrometopus huntleyi* (Coleoptera: Curculionidae) from the sub-Antarctic Prince Edward Island Archipelago.**

Key research questions:

Q1: Are there differences among populations of the newly described *B. huntleyi* on MI and PEI?

Q2: Are there one or more species present, as has been recorded for the genus *Ectemnorhinus* on the islands (Grobler *et al*. 2006)?

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In order to conserve, we need to know what we are conserving.

In order to make decisions we need to know what we are deciding about.