CHAPTER 6

Concluding comments on the Phylogenetic relationships and phylogeograpic patterns as observed within the *Ectemnorhinus*-group of weevils (Coleoptera: Curculionidae) from the sub-Antarctic Prince Edward Island Archipelago

The Prince Edward Island Archipelago (PEIA) has been the subject of intensive research for more than 60 years since its annexation by South Africa in 1948, (See Hänel & Chown 1999 and Chown & Froneman 2008 for a more information). When considering the species of the *Ectemnorhinus* group of genera endemic to the PEIA (Kuschel & Chown, 1995) that was known prior to this study, namely *Ectemnorhinus similis* (Waterhouse, 1885), *Ectemnorhinus marioni* (Jeannel, 1940), *Bothrometopus parvulus* (Waterhouse, 1885), *Bothrometopus elongates* (Jeannel, 1953), *Bothrometopus randi* (Jeannel 1953) and *Palirhoeus eatoni* (Waterhouse 1876), it can be seen that the last time new species, within the *Ectemnorhinus* group of genera on the PEIA, were identified was 57 years ago in 1953 by Jeannel. In this study we identified and described two new species within the *Ectemnorhinus* group of genera from the PEIA. The first is *Ectemnorhinus kussheli* that occurs only on PEI and the second is *Bothrometopus huntleyi* from both MI and PEI.

Using a combined molecular and morphometric approach the current study showed that *E. similis* (Waterhouse, 1885) and *E. marioni* (Jeannel, 1940) should be synonymized as *E. similis* as *E. similis* has priority. We found no evidence that weevils cluster on the basis of body size or according to plant species from which they were collected when analyzed phylogenetically. In addition, multivariate analyses of the MI samples showed no separation of *Ectemnorhinus* individuals according to previous suggested morphologically- and ecologically-defined distinguishing characteristics (Crafford et al. 1986; Chown and Scholtz 1989; Chown 1990). We also confirm that size variation is a major source of difficulty when attempting to establish species limits within the genus (see Brown 1964; Kuschel 1970, 1971; Crafford et al. 1986; Chown and Scholtz 1989; Chown 1990, 1991). While only one species of *Ectemnorhinus* weevils was found on MI, both the genetic and the morphometric analyses

indicated two size-distinct species on PEI with a sequence divergence value of 1.5 % that corresponds well with the intra-generic Kimura-2-parameter genetic distances of 1.5 % and 2.1 % reported for arthropods from other island systems (Trewick 2000). Because individuals from Prince Edward Island have not been used in formal taxonomic assessments (i.e. they have not been physically identified and labelled, with a corresponding description or specimen listing in the literature), the larger PEI-restricted weevils have been designated *E. kuscheli*. One possible reason for the different status of *Ectemnorhinus* species between the two islands may be due to differences in glaciation histories, as MI was extensively glaciated whilst PEI was not (Verwoerd 1971). As a result, weevils on PEI would have had longer exposure to vascular plants as an additional, more nutritious food source to bryophytes, than those on MI. This may have given rise to two species, a smaller one with a preference for bryophytes and a larger one with a preference for angiosperms, as suggested by Chown (1990). Another possible explanation for the dissimilar status of these island species may be due to differences in coalescence times. Results from this study indicate that the *Ectemnorhinus* weevils lineages coalesce at approximately 0.49 MYA on PEI, soon after the islands emerged, while coalescence on MI was dated to have occurred approximately 0.16 million years later.

When examining the population dynamics of *Ectemnorhinus* weevils on the PEIA, we see that PEI was colonized before MI. This is probably due to the fact that PEI was not glaciated like MI (Verwoerd 1971). The PEI population then acted as the source population for the colonization of MI by *Ectemnorhinus* weevils some time before the last glaciations where the weevils were able to colonize the whole of MI. The separation by distance of the PEI *Ectemnorhinus* weevils from those on MI then gave raise to two species by alopatric speciation, namely *E. kucheli* on PEI and *E. similis* on MI. During the last glaciation MI was extensively glaciated with only the southwestern corner of the island being free of ice. This extensive glaciation of MI would result in the eradication of all *E. similis* on MI except for those occurring on the ice-free southwestern corner of the island, of which a remnant population is still present on MI that are closer related to *E. kucheli* on MI than any other MI populations. We propose that at the end of the last glacial maximum, when the ice started to melt, the coastal areas of MI emerged first from beneath the ice and were available for the re-colonization of weevils. The movement of the weevils that were isolated in the south-western corner of MI, along the coastal areas of the island, was assisted by the strong, frequent south-western winds (Schulze, 1971). Subsequent Holocene post-glacial volcanism (Hall 1978, 1982, 2004) was then responsible for the fragmentation of the new migrants, to the rest of

MI, in small pockets surrounding by fresh, uninhabitable lava. The time it took for the different populations of isolated weevils to recover from the devastation of the lava as well as the time it took for the lava that isolated the weevils in small populations to become inhabitable for re-colonization of weevils, was sufficient for the weevils in each population to diverge from those in the other populations. When the Holocene black lavas became re-colonizeable the weevils from the different isolated populations could again migrate to the rest of the island. At present the members of the different genetically identified populations occur geographically in the same area and in some cases even on the same plant, but yet no noticeable gene flow was detected between them. We thus suggest that the time of isolation, before the Holocene post-glacial black lavas became hospitable, were long enough and that the populations were small enough that reproductive isolation could be induced to form a number of sub-species. We have recognised two sub-species of *E. kucheli* on PEI and seven sub-species of *E. similis* on MI. The fact that the living conditions and food available for all the different isolated populations were the same makes it not surprising that members of all the different sub-populations are morphologically indistinct.

When examining *B. huntleyi* we found that *Bothrometopus* weevils first colonised Marion Island at high altitude approximately 0.447 MYA where they were probably restricted to a small area through glaciation. Following a period of extended isolation, the data suggest that approximately 0.117 MY later, *B. huntleyi* dispersed to the remainder of Marion Island as well as over the 19 km stretch of sea to Prince Edward Island, at a time coinciding with glaciation-free volcanism. At present, the high elevation Marion Island founder population is intact and accompanied by two discrete population complexes separated by 19 km of sea on the two islands. Historical inter-island migration has been minimal and uni-directional (from Marion Island to Prince Edward Island only) and coincided with glaciation-free volcanic stages on Marion Island. It has also been revealed that *B. huntleyi* individuals from Prince Edward Island are genetically more similar to each other than to individuals from Marion Island. It is therefore likely that these allopatric populations will continue to diverge as long as the natural inter-island isolation is maintained.

We then examined 13 species from the genera *Palirhoeus* Kuschel, *Bothrometopus* Jeannel, and *Ectemnorhinus* G.R. Waterhouse from 22 populations from Marion Island, Prince Edward Island, Heard Island, Kergeulen Island and Possession Island. These genera are all within the *Ectemnorhinus* group of genera (Kuschel & Chown, 1995). Although this is only a partial analysis of this group of weevils, the study has cast significant light on the evolution and biogeography thereof, with important implications for interpretation of biogeographic

and evolutionary dynamics in the region more generally. Perhaps the most significant point to emerge is that colonization of the Prince Edward Islands is likely to have taken place repeatedly from other islands in the South Indian Ocean Province. We also suggest that the genus *Palirhoeus* is clearly not readily distinguishable on a mtCOI sequence basis from the genus *Bothrometopus*, thus questioning the retention of the species *P. eatoni* in a separate genus, and its position in Kuschel & Chown's (1995) phylogeny as basal to the genera *Bothrometopus* and *Ectemnorhinus*. The two species groups in the genus *Bothrometopus* (*fasciatus* group and *gracilipes* group) identified on morphological grounds by Kuschel & Chown (1995) also do not have support on an mtCOI basis.

Conservation recommendations

An important conservation biogeographic (see Whittaker *et al*. 2005) insight from our work is that anthropogenic gene flow between populations on Marion Island and Prince Edward Island should be prevented. Thus, the current practise of limiting visits to Prince Edward Island to a minimum, and the strict quarantine provisions for such visits (e.g. Anonymous 1996, Davies *et al*. 2007) should be maintained. Moreover, the genetic distinctiveness of the weevil populations on Marion Island, which is under threat via increased size-selective predation by the house mouse, *Mus musculus domesticus* (Gleeson & van Rensburg 1982, Chown & Smith 1993, Smith *et al*. 2002; Jansen van Vuuren & Chown 2007), also underscores the need to control mice (see Angel *et al*. 2009) on Marion Island to ensure that both the unique genetic variation on Marion Island, and the evolutionary dynamics of the archipelago are conserved.

Future research

There are numerous studies left to be done on the *Ectemnorhinus* group of genera. We are only highlighting a few:

We suggest further comprehensive molecular phylogenetic analyses of the biogeography of the region including all the species in the *Ectemnorhinus* group of genera as this would give the complete picture.

As the population study of the *Ectemnorhinus* weevils gave many new insights on biogeography and species dynamics, the same studieds from the other species on the PEIA might give us an even clearer picture of the biogeography of the islands.

More extensive sampling from all areas of PEI is needed in order to give a complete picture of the biogeography on PEI.

We suggest that breeding experiments between individuals from the different sub-species of *E. kucheli* on PEI and of *E. similis* on MI should be undertaken to determine whether they are unable to interbreed or whether there are some external factors that prevent gene flow to occur between them.

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