

Morphometric changes over time in weevils (Coleoptera: Curculionidae) from the sub-Antarctic Marion Island: An analysis based on mire sediment sub-fossil remains and recent samples

Abstract Sub-fossil weevil elytra and head capsule remains were recovered in mire sediments from depths ranging between 2.5 m to 2.0 m on the sub-Antarctic Marion Island. The weevil remains from 2.5 m and 2.0 m were carbon-dated to be from 2331 BC and 789 BC, respectively, representing a period considered to pre-date the potential effects of global warming from the green-house effect and predation by house mice (*Mus musculus*, sensu lato) that were introduced on Marion Island in the early 1800s. Head capsules, being the best preserved sub-fossil components, formed the basis of the analyses in this study. Three head capsule measurements were used to: 1) distinguish between the six currently recognised weevil species on Marion Island; 2) identify sub-fossil material; and 3) assess morphometric changes over time. Based on the head capsule data, sub-fossil weevil remains were identified as belonging to the genus *Ectemnorhinus* and were compared to recent samples collected in 1986/87 and 2001 from *Blepharidophyllum* mire communities. The analyses showed no statistically significant morphometric size and shape changes in sub-fossil material examined. However, head capsule measurements exhibited significant differences between sub-fossil material collected at different depths (2.0 – 2.5 m) and recently collected material (0 m), spanning a period of 4332 years. In addition, the overall size-related principal components (PCA) I and a single head capsule measurement decreased significantly from 2331 BC to the present (1986/87 and 2001). These results are interpreted with reference to the potential effect of climate change and size-selective predation by the house mouse.

Key words: Weevils, sub-fossils, morphometric changes over time, climate change, mouse predation, sub-Antarctic Marion Island

Running title: Morphometric changes over time in sub-fossil weevil remains and recent samples from sub-Antarctic Marion Island

Introduction

Terrestrial environments are facing significant threats due to climate change, invasive species and habitat fragmentation (Dukes and Mooney 1999; Mack et al. 2000; Luck et al. 2004). For example, biological invasions constitute one of the most important conservation threats to the functioning of ecologically sensitive ecosystems, such as the isolated sub-Antarctic South Indian Ocean Province Islands (Bonner 1984; Chown et al. 1998; Bergstrom and Chown 1999). In addition, various studies have demonstrated that species are already exhibiting changes in population densities, distributional ranges and morphology as a result of global climate change (for examples, see Lawton 1995; Parmesan 1996; Kuchlein and Ellis 1997; Parmesan et al. 1999; Hughes 2000; Huyser et al. 2000).

These include studies that have alluded to potential anthropogenic factors that may cause changes in weevil morphology on the sub-Antarctic Marion and Prince Edward Islands that in turn, affect their ecosystem functioning (Smith 1987; Chown and Smith 1993; Smith and Steenkamp 1993; Smith et al. 2002; van Aarde et al. 2004). The suggested anthropogenic factors include the potential effect of climate change from the green-house effect and predation by mice that were introduced on Marion Island in the early 1800s, but not on the neighbouring Prince Edward Island that is located 22 km to the north-east of Marion Island (Watkins and Cooper 1986).

This led to the investigation of the potential impact of climate change and mice predation on two mouse-preferred weevil prey species, *Ectemnorhinus marioni* and *E. similis* from *Azorella selago*-dominated habitats on both Marion and the mouse-free Prince Edward Islands (Chown and Smith 1993). The results of this study suggest a tendency towards a reduced body length in samples collected over a six-year period between 1986 and 1992 (Chown and Smith 1993). Chown and Smith (1993) and subsequently, Smith et al. (2002) suggested that this body size reduction in *Ectemnorhinus* species may be attributed to size-selective predation of these mouse-preferred prey species. These studies reported that mice prefer large-sized weevils to such an extent that mouse-predation pressure may be responsible for changes in mean body length and size-class distributions in *Ectemnorhinus* weevil prey species (Chown and Smith 1993; Smith et al. 2002).

Mouse populations on Marion Island have been reported to be temperature-dependent, such that increased island temperature may escalate mouse populations (Smith and Steenkamp 1990; Smith 2002), which in turn would lead to a decrease in weevil populations via predation (Crafford and Scholtz 1987; Chown and Smith 1993). Decreased weevil populations will in turn lead to a decrease in overall rates of nutrient cycling, leading to imbalances between

primary production and decomposition (Smith and Steenkamp 1990). It has been documented that mice numbers have increased since 1979 (Matthewson et al. 1994; van Aarde et al. 1996) and the contribution of weevil adults to mice diet have also increased considerably (Smith et al. 2002), posing a significant threat to weevil species, more especially *E. similis*, *E. marioni*, *Bothrometopus randi* and *B. parvulus* (Chown and Smith 1993).

However, other studies suggest that the effect of ameliorating temperatures on Marion and Prince Edward Islands as a result of global warming may have a significant impact on weevil morphometric size and shape (see Chapter 4). The two islands offer ideal ecosystems to study the responses of weevil species to changing global climate and/or biological invasions, through morphometric size and shape changes. The two islands, separated by 22 km and assuming similar temperature increases on both islands, and that only Marion Island is colonised by mice (Watkins and Cooper 1986; Crafford and Scholtz 1987), excludes mice predation as a potential influential factor on morphometric changes on Prince Edward Island weevil species. Similar morphometric size and shape changes on other weevil species (*B. randi*, *B. parvulus*, *B. elongatus* and *Palirhoeus eatoni*) on both Marion Island and Prince Edward Island, suggest that climate change may play a primary role in weevil morphological changes over time (see Chapter 4).

Over the last 50 years, mean surface air temperature on Marion Island has increased by $0.025^{\circ}\text{C year}^{-1}$ while precipitation decreased (Smith and Steenkamp 1990; Smith 1991, 2002; Weimerskirch et al. 2003). As a result, Marion Island's ecosystem functioning is in the process of changing, with elevated temperatures expected to increase productivity as well as nutrient demand (Smith 1988; Smith 2002). Energy flow and nutrient cycling are mainly dependent on soil macro-invertebrates (Crafford 1990; Smith and Steenkamp 1992). The activities of these organisms are strongly temperature-dependent (Chown et al. 1997; Klok and Chown 1997) and the effect of temperature on insect body size, with increasing temperature may promote smaller-sized individuals to be produced (Atkinson 1994; James et al. 1997; Karan et al. 1998). While these potential influences may be valid, the partitioning of potential causal effects of morphological change over time has been complicated further by the problematic taxonomic status of the two *Ectemnorhinus* species that have traditionally been considered to occur on both islands. An attempt was made to resolve this taxonomic problem using parallel and complementary molecular and morphometric techniques. In contrast to the previous taxonomy, both molecular and morphometric analyses suggest the presence of two genetically distinct species on Prince Edward Island, but only a single species that comprises diverse genetically discrete populations on Marion Island (see Chapter 3). This has led to the *Ectemnorhinus* species occurring on Marion Island to be referred to as an *Ectemnorhinus* species complex.

In the present study, the identity of sub-fossil remains that were recently sampled from mire habitats on Marion Island are first determined with reference to the current insight into the taxonomy of weevil species occurring on both Marion and Prince Edward Islands. These sub-fossil weevil remains, sampled from different depths (2.0 – 2.5 m) considered to represent different dimensions in time and space, together with recently collected *Ectemnorhinus* samples from mire habitats on Marion Island, are in turn used to assess if morphometric changes have occurred in these weevils over time.

By so doing, the hypothesis is that should sub-fossil weevil remains represent the same currently recognised species in mire habitats, then sub-fossil remains from the two sampled depths should not show significant morphological changes in remains from this period that pre-dates the potential effect of mouse-predation and/or global warming. The prediction is that sub-fossil remains from Marion Island should differ morphologically from material collected recently from a period characterised by the potential effect of mouse-predation and/or global warming.

Materials and methods

Study area and samples

Two core samples (50 cm in length) were collected in April 2002 from a mire community, mire samples A (46°52.730'S; 37°50.916'E) and B (46°52.676'S; 37°51.078'E) on Marion Island using a 7 cm x 50 cm Russian corer. Each core was 2.5 m deep.

Twenty-five 2 cm pieces were recovered from each core sample at depths between 2.0 and 2.5 m, separately washed and sieved to remove excess organic matter, fine-grained mud and stones. Weevil body parts were removed and stored in 100% ethanol. A total of 41 and 51 elytra were recovered from mire samples A and B, respectively. However, the recovered elytra could not be used for morphometric analyses because of their crumpled and soft nature. Thirty-two and 31 weevil head capsules were recovered from mire samples A and B, respectively. Due to damage, a total of 57 sub-fossil head capsules were ultimately measured from both mire samples A and B.

Currently recognised *Ectemnorhinus* weevil species were collected by hand (L. Janse van Rensburg) from *Blepharidophyllum densifolium* (Hook.) Angstr. (Scapaniaceae) mires on Marion Island during 2001. A total of 34 individuals were sampled, stored in absolute ethanol, and head measurements recorded. Additional *Ectemnorhinus* specimens ($n = 33$) collected from *Blepharidophyllum densifolium* (Hook.) Angstr. (Scapaniaceae) mires on Marion Island

during 1986/87 (S.L. Chown) were included in the analyses to assess morphometric changes over time.

Morphometric measurements

Head capsule measurements were recorded to the nearest 0.01 mm (O, A and AD). All measurements were recorded by a single observer (L. J. van Rensburg) using a stereo microscope fitted with a calibrated eye-piece micrometer. These variables defined and illustrated by Janse van Rensburg et al. (2003) include: inter-ocular distance (O), inter-antennal distance (A) and antenna/eye diagonal (AD).

Carbon-dating

The age of weevil elytra sampled in the mires were determined through the services of Quadru – Environmentek, Centre for Industrial Research (CSIR), Pretoria, South Africa in collaboration with the radio-carbon station at Groningen University, Netherlands, Salisbury and Isotopes Inc., USA. Analysis included AMS Date based on 5 mg samples, and was conducted in collaboration with CIO, Groningen, Netherlands. Dating was based on years Before Present (BP) (i.e., before AD 1950) in conventional radio-carbon years based on a half-life of 5568 years for C¹⁴. Ageing was corrected for variations in isotope fractionation, and was calibrated for the southern hemisphere using a 2000 up-dated version of the PRETORIA computer programme (Talma and Vogel 1993).

Statistical analyses

Delineation of currently recognised weevil species from Marion Island based on head capsule measurements

Janse van Rensburg et al. (2003) showed that a selected set of 15 measurements is sufficient to distinguish between recent samples of currently recognised weevil species from Marion Island. In the present study, however, only three measurements could be recorded on weevil head capsules collected in core samples. Consequently, the original morphometric dataset used by Janse van Rensburg et al. (2003) was re-analysed using the three recordable head capsule measurements to assess if they were sufficient to distinguish recent samples of all currently recognised weevil species from Marion Island.

The three head capsule measurements were subjected to the same series of multivariate analyses used by Janse van Rensburg et al. (2003). These analyses included: 1) principal components analysis (PCA) based on among-character product-moment correlation coefficients; 2) unweighted pair-group arithmetic average (UPGMA) cluster analysis computed from both, among-operational taxonomic units (OTUs; Sneath and Sokal 1973) euclidean distances and product-moment correlation coefficients (Pimentel and Smith 1986; Rohlf 1986); and 3) canonical variates (discriminant) analysis (CVA; Sneath and Sokal 1973) based on data from years with adequate sample sizes followed by a multivariate analysis of variance (MANOVA; Zar 1996) to test for statistically significant differences between groups.

Identification of sub-fossil samples from Marion Island

The identification of sub-fossil material was based on both PCA and UPGMA cluster analysis using the three head capsule measurements. These analyses, however, included a subset of the data from the original dataset used by Janse van Rensburg et al. (2003) to distinguish recent samples of all currently recognised weevil species from Marion Island, but only focussed on the three head capsule variables.

Analysis of morphometric changes over time

The multivariate PCA, UPGMA cluster analysis and CVA based on the three head capsule measurements were used to assess morphometric size and shape changes over time using both core samples and recently collected mire material (1986/87 and 2001). Kruskal-Wallis analysis of variance (ANOVA; Zar 1996) was used to assess morphometric changes over time using the three head capsule measurements and the overall size-related PCA I independently across all depths and was based only on core depth samples with $n \geq 3$. In addition, a dataset consisting only of the four known sampling times (2331 BC; 789 BC; 1986/87 and 2001) were subjected to Kruskal-Wallis analysis of variance (ANOVA; Zar 1996). Dunn's post hoc analyses (Zar 1996) were used to determine significant differences between sampling years. Mean \pm Standard Error (SE) at each depth as well as percentage head capsules recovered in all depths were calculated for each of the three head capsule measurements independently. Patterns of variation were also evaluated by Spearman's rank correlation analysis (Zar 1996) of PCA I scores and individual head capsule measurements (O, A and AD) with depth, representing time.

All statistical analyses were performed using various univariate and multivariate algorithms available in STATISTICA version 5.5 (Statsoft 1995).

Results

Carbon-dating

Since core samples were collected in similar mire communities, only elytra sampled in mire sample A were used for carbon-dating. Carbon-dating results are presented in Table 1 as 1-sigma range, together with the most probable date (in parentheses). These results indicate that the sediment sequence of core A (2.0 – 2.5 m) spans 1542 years, with elytra sampled at 2.0 m being from 789 years BC, and elytra sampled at 2.5 m being from 2331 years BC (Fig. 1).

Table 1 Radiocarbon analysis results given in years Before Present (BP), i.e. before AD1950. Indicated in superscript are: ¹Laboratory analysis number; ²Sample number; ³Dates reported in conventional radiocarbon years (i.e., using a half-life of 5568 years for C ¹⁴ and ages corrected for variations in isotope fractionation); and ⁴ 1-sigma range, with the most probable date between parentheses

Anal. ¹ No. GrA-	Sample ² designation	$\delta^{13}\text{C}$ (‰PDB)	Radiocarbon ³ Age yrs BP	Calibrated ⁴ Date
24396	A 1:1 (2.0 m)	-25.0	2610 ± 45	801 (789) 774 BC
24394	A 25:2 (2.5 m)	-21.4	3910 ± 40	2447 (2331) 2287 BC

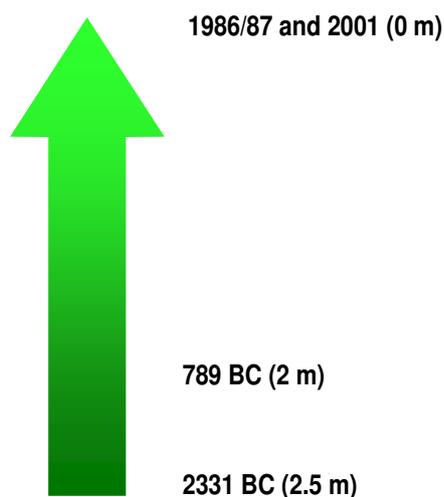


Fig. 1 Sampled mire depths (m) with respective times indicated

The results of both PCA and UPGMA cluster analysis undertaken to assess if the three recordable head capsule measurements were sufficient to distinguish recent samples of currently recognised weevil species, were broadly similar and are best exemplified by the results of the former series of analyses. Separation of all six species, based on three head capsule measurements are best illustrated by the first (92.02% variance) and second (6.33% variance) PCA axes (Fig. 2a; Table 2a). On the first PCA axis *B. elongatus*, *P. eatoni* and *B. randi* are separated, in addition to *E. marioni* and *B. parvulus* separating from *E. similis* (Fig. 2a). All three head measurements showed positive, high loadings on the first PCA axis, with measurement O contributing the most to the separation (Table 2a). Although most species show overlap, the PCA in the present study closely resembles the original PCAs in Janse van Rensburg et al. 2003 (Chapter 2; see Fig 4a-c). Therefore, despite the partial overlaps, these results suggest that the three head capsule measurements may be used to distinguish between the six currently recognised weevil species from Marion Island, particularly when interpreted with reference to the results of the previous analyses by Janse van Rensburg et al. (2003) based on 15 measurements.

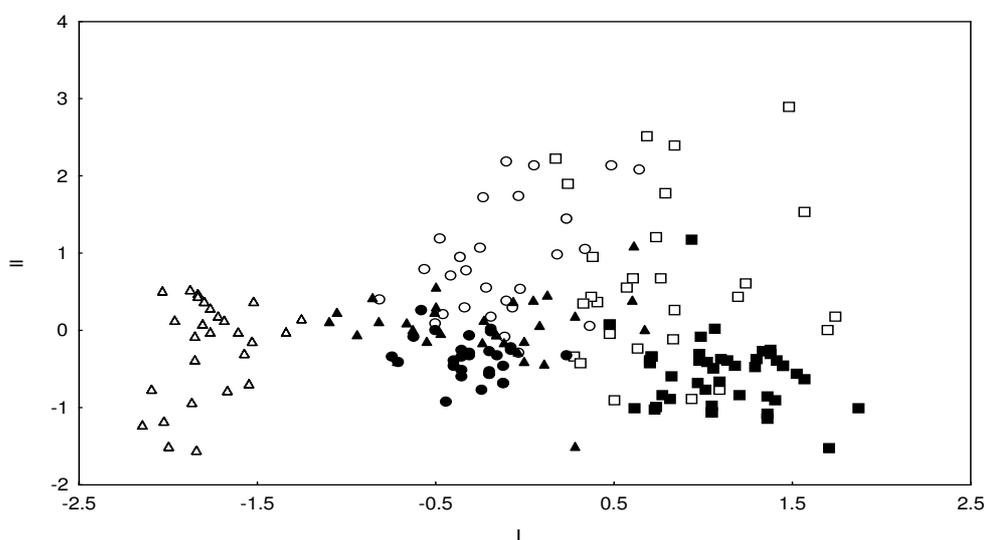


Fig. 2a The first two components from a principal components analysis (PCA) using three head capsule measurements of *Palirhoeus eatoni* (unfilled circle), *Ectemnorhinus marioni* (filled circle), *E. similis* (filled square), *Bothrometopus randi* (unfilled square), *B. parvulus* (filled triangle), and *B. elongatus* (unfilled triangle) from sub-Antarctic Marion Island

Table 2 Loadings of variables on components I, II and III from principal components analyses (PCA) of head capsule measurements to a) distinguish between six currently recognised weevil species on Marion Island using data from Janse van Rensburg et al. (2003) and b) of a combination of the six currently recognised weevil species together with mire core samples from Marion Island

	Measurement	PCA I	PCA II	PCA III
a)	O	0.975	-0.155	-0.162
	A	0.933	0.360	0.011
	AD	0.970	-0.191	0.152
	% trace	92.02	6.33	1.65
b)	O	0.971	-0.185	-0.153
	A	0.922	0.386	-0.001
	AD	0.971	-0.182	0.154
	% trace	91.22	7.21	1.58

Identification of sub-fossil samples from Marion Island

The results of both PCA and UPGMA cluster analysis based on three head capsule variables, undertaken to identify sub-fossil material in the mire core with reference to recent samples of currently recognised weevil species, were broadly similar and are best exemplified by the PCA results. The sub-fossil weevil head capsules sampled in the mire core cluster with the currently recognised *E. similis* and *E. marioni* (Fig 2b). PCA axis I accounted for 91.22% of the total variance with PCA axis II contributing 7.21% of the total variation (Table 2b). High loadings are exhibited by all measurements, with O and AD equally contributing to the separation (Table 2b).

However, both molecular and morphometric analyses suggest the presence of a single *Ectemnorhinus* species that comprises diverse genetically discrete populations on Marion Island (see Chapter 3). Considering that the *Ectemnorhinus* species occurring on Marion Island has been referred to as an *Ectemnorhinus* species complex, these results suggest that the sub-fossil head capsules sampled on Marion Island may belong to the genus *Ectemnorhinus*.

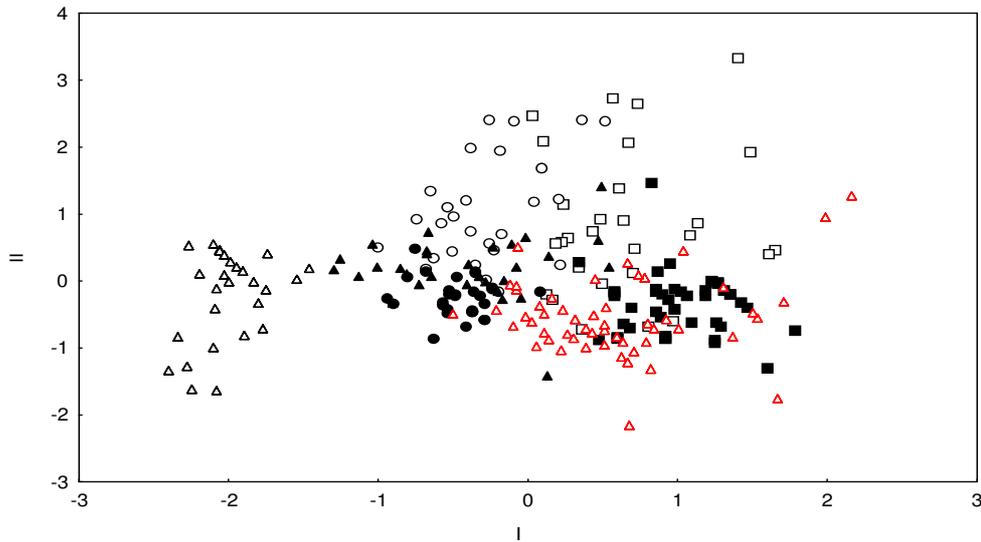


Fig. 2b The first two components from a principal components analysis (PCA) using three head capsule measurements of *Palirhoeus eatoni* (unfilled circle), *Ectemnorhinus marioni* (filled circle), *E. similis* (filled square), *Bothrometopus randi* (unfilled square), *B. parvulus* (filled triangle), *B. elongatus* (unfilled triangle), and sub-fossil mire head capsules (red triangle) from sub-Antarctic Marion Island

Analysis of morphometric changes over time

The results of both PCA and UPGMA cluster analysis based on three head capsule variables undertaken to simultaneously assess morphometric size and shape changes over time using both core samples and recently collected mire material were broadly similar and are best exemplified by the former series of analyses. There is no morphological size and shape separation between sub-fossil weevil head capsules and *Ectemnorhinus* species collected in *Blepharidophyllum* mires in 1986/87 and 2001 (Fig. 3a), suggesting no morphological changes over time. Similarly, there is no morphological size and shape separation between sub-fossil material collected at different depths that are considered to represent different dimensions in time and space (results not illustrated).

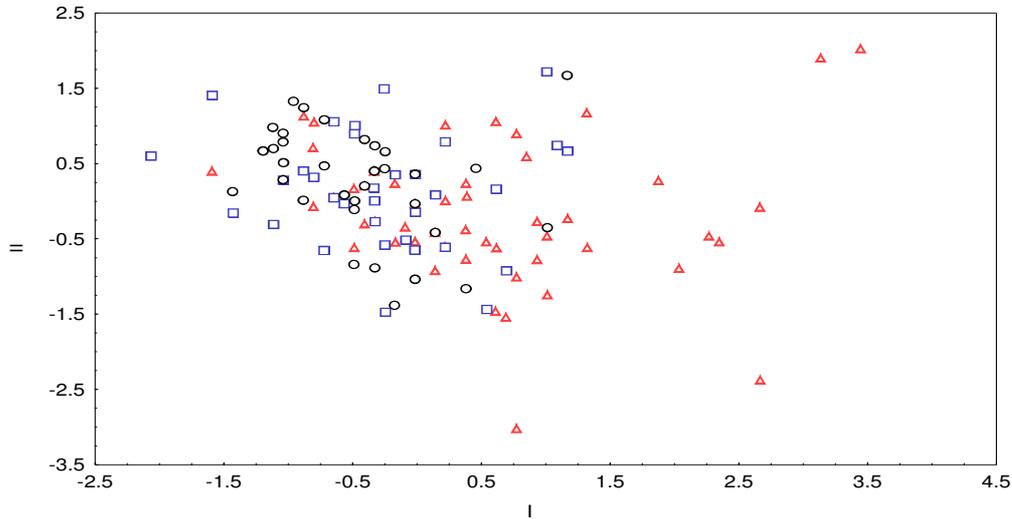


Fig. 3a The first two components from a principal components analysis (PCA) using three head capsule measurements of *Ectemnorhinus* weevil species collected in *Blepharidophyllum* mire communities in 1986/87 (black circles), 2001 (blue square), and sub-fossil mire head capsules (red triangle) from sub-Antarctic Marion Island

Data that included *Blepharidophyllum* mires in 1986/87, 2001 and carbon-dated sub-fossil core samples, was further analysed using canonical variates analysis (CVA). Ideally, head measurements from both the carbon-dated core samples (2.5 m; 2331 BC and 2.0 m; 789 BC) were considered for analyses. However, sample size from the 2.0 m depth were too small for CVA, thereby only 2.5 m (2331 BC) together with 1986/87 and 2001 samples were analysed using CVA (Fig. 3b). In contrast to the PCA, the 2331 BC sample separates from the recently collected material on axis I (MANOVA: $F_{6,132} = 3.48$; $n = 71$; $P < 0.01$) (Fig. 3b), with O contributing to most of the differences (Table 3).

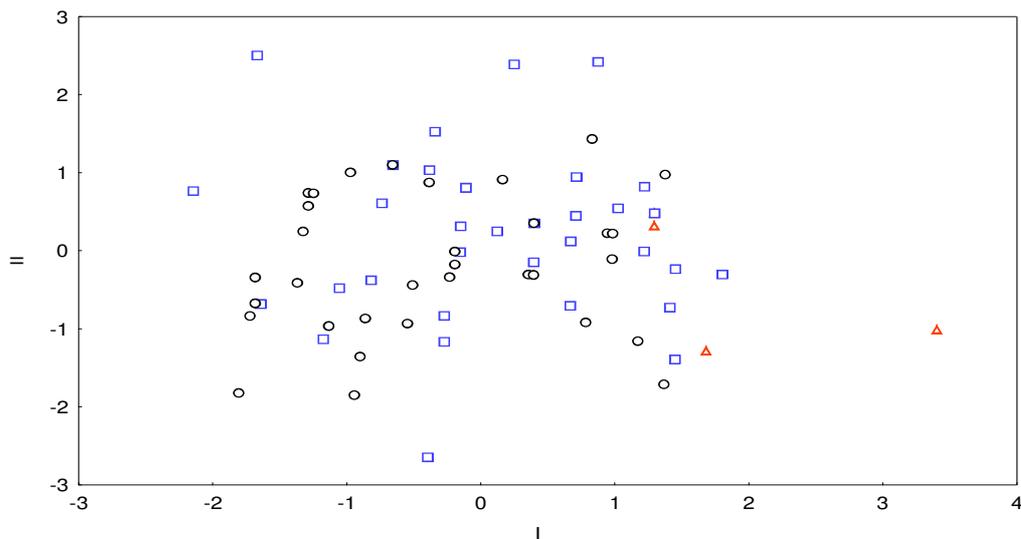


Fig. 3b The first two components from a canonical variates analyses (CVA) using three head capsule measurements of *Ectemnorhinus* weevil species collected in *Blepharidophyllum* mire communities in 1986/87 (black circles), 2001 (blue square), and 2331 BC (red triangle) from sub-Antarctic Marion Island

Table 3 Loadings of variables on canonical variate axes I and II from a canonical variates analysis (CVA) of head capsule measurements of weevil samples collected in *Blepharidophyllum* mire communities in 1986/87, 2001 and 2331 BC from sub-Antarctic Marion Island

Measurement	CVA I	CVA II
O	1.103	0.924
A	0.002	0.478
AD	-0.143	-1.715

Descriptive statistics (mean \pm SE) showed a tendency in all three head measurements (O, A and AD), for samples pre-dating the effects of global warming and the introduction of mice on Marion Island (2.5 m; 2331 BC and 2.0 m; 789 BC), to have larger head capsule measurements than recent samples (1986/87 and 2001) collected at 0 m (Table 4). The complete dataset ($n = 110$), with different depths representative of different times (i.e., 2.0 m up to 2.5 m representing a time period of 1542 years and 0 m (1986/86 and 2001 representing present time), indicated significant differences for measurement O ($H_{10,115} = 24.71$; $P < 0.01$), A ($H_{10,115} = 17.96$; $P < 0.05$) and AD ($H_{10,115} = 24.29$; $P < 0.01$) between recent and sub-fossil data.

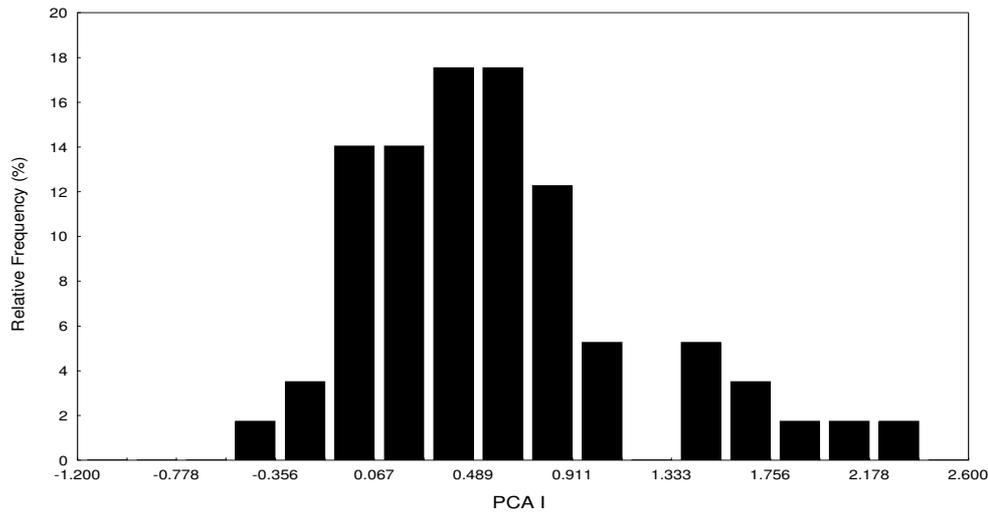
In addition, a dataset consisting only of known times (i.e., 2331 BC: 2.5 m; 789 BC: 2.0 m; 1986/87: 0 m; and 2001: 0 m), showed only measurement O ($H_{4,72} = 13.25$; $P < 0.01$; Dunn's post hoc test: between 2331 BC and 1986/87) and PCA I ($H_{4,72} = 9.54$; $P < 0.05$; Dunn's post hoc test: between 2331 BC and 2001), to be significantly different over time, whereas measurement A ($H_{4,72} = 5.28$; $P = 0.15$) and AD ($H_{4,72} = 7.44$; $P = 0.06$) showed no statistically significant differences between known sampling years. The largest number of weevil head capsules was sampled between 2.14 m and 2.44 m (Table 4). This may be indicative of a higher quality of preserved material at deeper strata within core samples.

Table 4 Mean \pm Standard Error (SE) values for inter-antennal distance (A), inter-ocular distance (O) and antenna/eye diagonal (AD) for 57 sub-fossil head capsules sampled in mire communities (Mire samples A and B combined). Percentage heads sampled at different depths are indicated. Head measurements for individuals collected in 1986/87 and 2001 in *Blepharidophyllum* mires are included

Piece number	Depth (m)	Mean O (mm) \pm SE	Mean A (mm) \pm SE	Mean AD (mm) \pm SE	<i>n</i>	% occurrence
<i>Blepharidophyllum</i> mire (2001)	0	0.49 \pm 0.01	0.32 \pm 0.01	0.47 \pm 0.01	34	
<i>Blepharidophyllum</i> mire (1986/87)	0	0.47 \pm 0.00	0.31 \pm 0.00	0.47 \pm 0.00	33	
1	2.00-2.02	0.55 \pm 0.09	0.41 \pm 0.15	0.56 \pm 0.13	2	3.51
2	2.02	0.52 \pm 0.02	0.38 \pm 0.00	0.47 \pm 0.02	3	5.26
5	2.08	0.67 \pm -	0.38 \pm -	0.58 \pm -	1	1.75
6	2.1	0.61 \pm -	0.29 \pm -	0.60 \pm -	1	1.75
7	2.12	0.53 \pm 0.01	0.35 \pm 0.02	0.48 \pm 0.02	5	8.77
8	2.14	0.51 \pm 0.01	0.33 \pm 0.00	0.47 \pm 0.01	7	12.28
9	2.16	0.48 \pm 0.03	0.33 \pm 0.00	0.45 \pm 0.05	2	3.51
10	2.18	0.54 \pm 0.01	0.36 \pm 0.04	0.52 \pm 0.01	3	5.26
11	2.2	0.51 \pm 0.02	0.33 \pm 0.01	0.51 \pm 0.02	6	10.53
13	2.24	0.50 \pm -	0.31 \pm -	0.48 \pm -	1	1.75
14	2.26	0.51 \pm -	0.33 \pm -	0.49 \pm -	1	1.75
15	2.28	0.56 \pm -	0.36 \pm -	0.52 \pm -	1	1.75
16	2.3	0.50 \pm -	0.32 \pm -	0.52 \pm -	1	1.75
19	2.36	0.49 \pm 0.04	0.33 \pm 0.05	0.47 \pm 0.05	2	3.51
20	2.38	0.54 \pm -	0.33 \pm -	0.51 \pm -	1	1.75
21	2.4	0.57 \pm 0.04	0.37 \pm 0.05	0.52 \pm 0.05	3	5.26
22	2.42	0.49 \pm -	0.32 \pm -	0.47 \pm -	1	1.75
23	2.44	0.53 \pm 0.00	0.34 \pm 0.00	0.49 \pm 0.00	8	14.04
24	2.46	0.50 \pm 0.02	0.30 \pm 0.02	0.41 \pm 0.01	4	7.02
25	2.48-2.50	0.57 \pm 0.01	0.35 \pm 0.02	0.52 \pm 0.03	4	7.02

Frequency distributions of sub-fossil (Fig. 4a) and recently collected (1986/87 and 2001) *Blepharidophyllum* mire (Fig. 4b) samples based on the scores of the first, morphometric size-related PCA axis show a tendency for recent samples to be smaller than sub-fossil material. A Kruskal-Wallis ANOVA, showed that differences between sub-fossil and recent sample PCA I scores are statistically significant ($H_{10,115} = 25.52$; $P < 0.01$; $n = 110$).

a



b

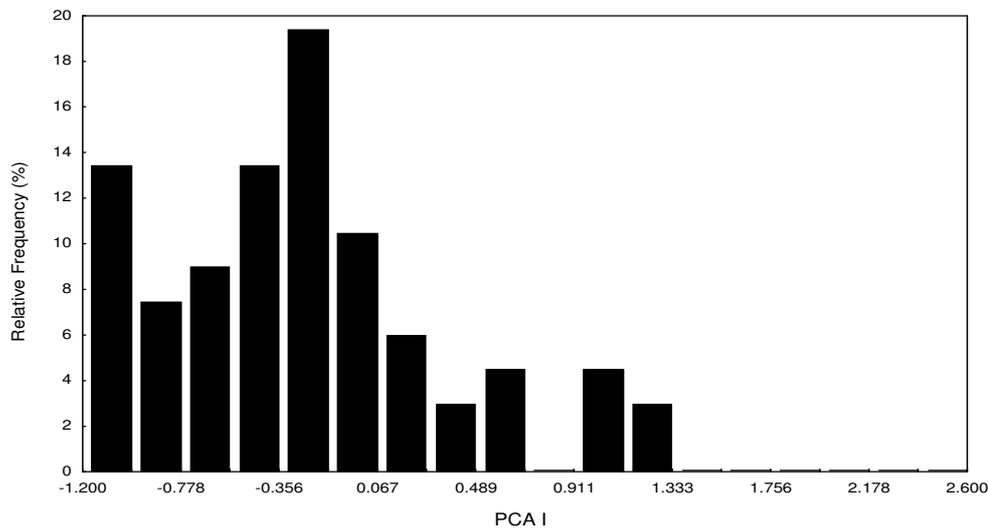


Fig. 4 Percentage relative frequency for principal component I, representing size, of **a** sub-fossil mire head capsules and **b** recently collected *Ectemnorhinus* samples (1986/87 and 2001) from sub-Antarctic Marion Island *Blepharidophyllum* mire communities

Correlations of PCA I scores (Fig. 5a) and individual head capsule measurements (Fig 5b-d) against all depths sampled (Table 5a) and for all depths of known age (Table 5b) indicated a negative and highly significant relationship in size from 2331 BC (2.5 m) to present time (0 m).

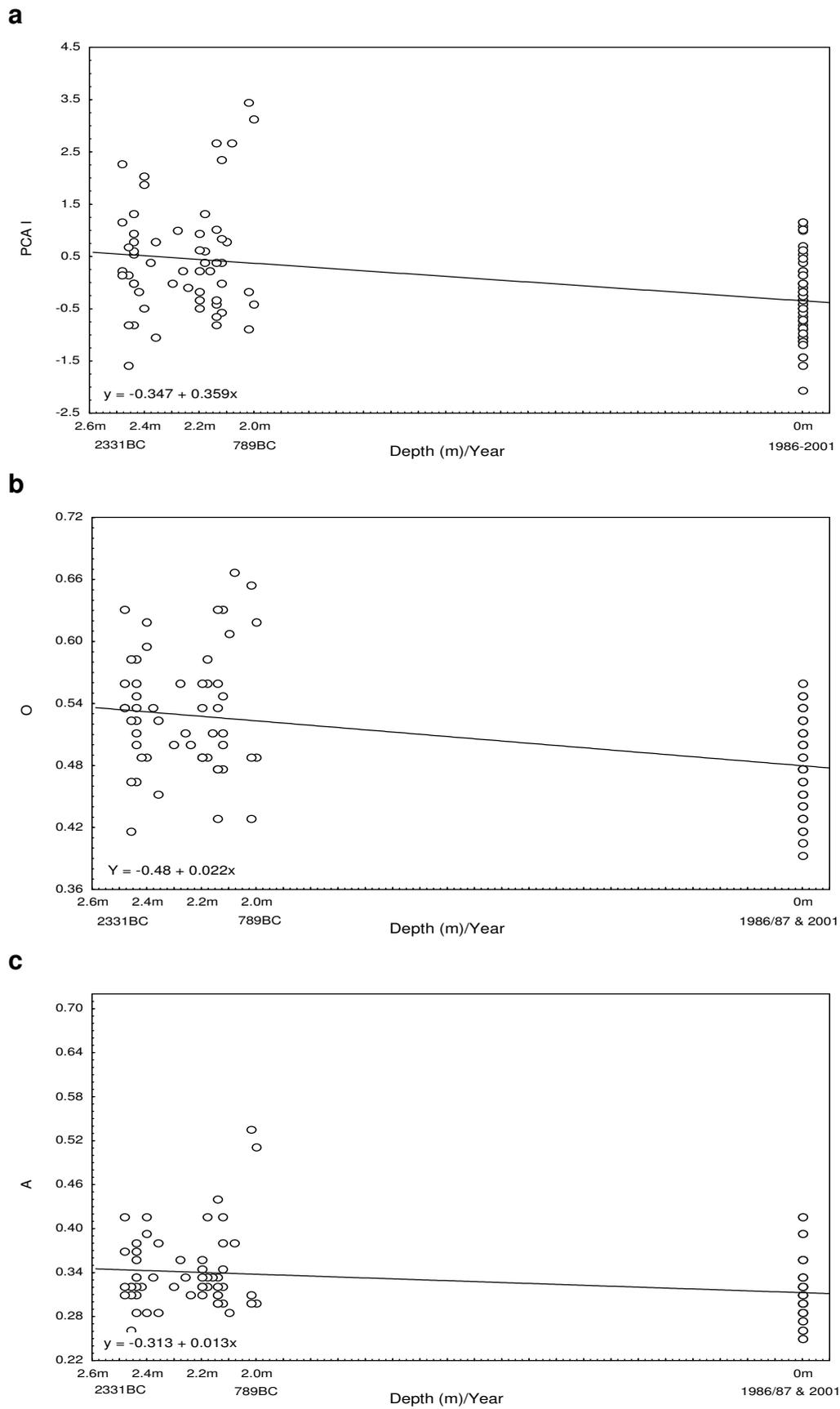


Fig. 5 Relationship between **a** principal component I (PCA I), indicative of overall size **b** measurement O **c** measurement A and depth (m)/year for sub-fossil and recently collected (1986/87 and 2001) *Ectemnorhinus* species in mire habitats. 0 m represents present time (1986/87 and 2001), with core samples collected at 2.0 m representing 789 BC and 2.5 m representative of 2331 BC

d

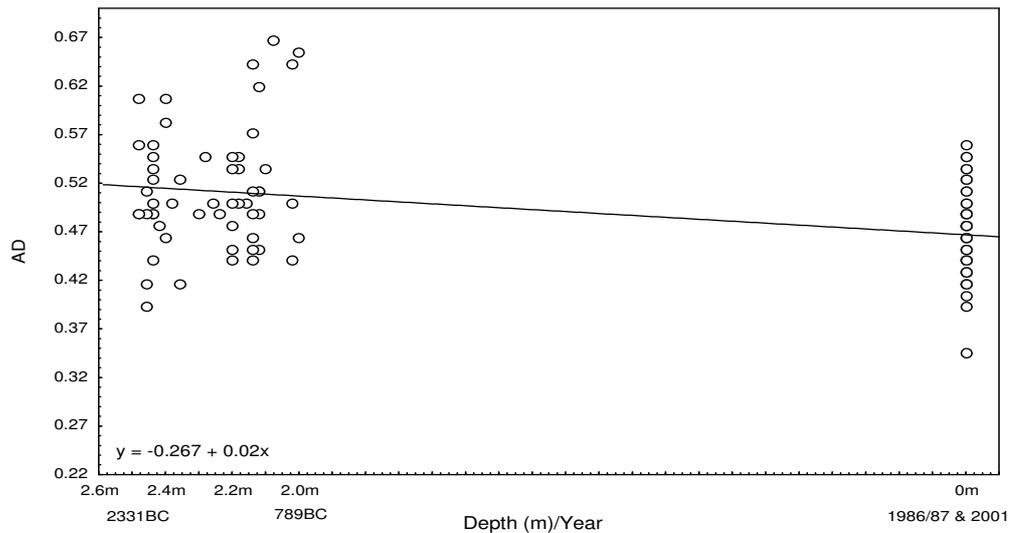


Fig. 5d Relationship between measurement AD and depth (m)/year for sub-fossil and recently collected (1986/87 and 2001) *Ectemnorhinus* species in mire habitats. 0 m represents present time (1986/87 and 2001), with core samples collected at 2.0 m representing 789 BC and 2.5 m representative of 2331 BC

Table 5 Results of correlations of the size-related variable, principal component I and three head capsule measurements (O, A and AD) for a) all depths for which samples were collected, including 0 m (1986/87 and 2001) representing present time ($n = 124$); and b) for all depths for which time estimates were obtained (2331 BC, 789 BC, 1986/87 and 2001) ($n = 73$). Sub-fossil and recently collected (1986/87 and 2001) *Ectemnorhinus* species were collected in *Blepharidophyllum* mires. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

Variable	Correlation coefficient (r)
a) Principal component I	-0.42 ***
O	-0.44 ***
A	-0.31 ***
AD	-0.41 ***
b) Principal component I	-0.48 ***
O	-0.45 ***
A	-0.42 ***
AD	-0.45 ***

Discussion

Body size changes of weevil populations from Marion and Prince Edward Islands may have serious consequences for island ecosystem functioning (Smith 1987; Smith and Steenkamp 1993; Smith et al. 2002). So far, studies suggest that *Bothrometopus randi*, *Palirhoeus eatoni*,

Ectemnorhinus similis and *E. marioni* from both Marion and Prince Edward Islands are exhibiting morphometric body size changes over time (Chown and Smith 1993; see Chapter 4).

However, the taxonomic status of *Ectemnorhinus* species occurring on both Marion and Prince Edward Islands has largely been uncertain (Kuschel 1971; Crafford et al. 1986; Chown 1990) precluding an insight into the morphological changes in this group of weevils. Nevertheless, a recent multi-faceted genetic and morphometric study (Chapter 3) suggests the presence of a single species of *Ectemnorhinus* species on Marion Island and the presence of two *Ectemnorhinus* species on Prince Edward Island. These *Ectemnorhinus* species also exhibit a wide range of body size variation as is the case with *Ectemnorhinus* species occurring on Heard and Kerguelen Islands (Kuschel 1970).

While the analyses in the present study suggest that the sub-fossil remains recovered from core mire depths on Marion Island are likely to belong to the genus *Ectemnorhinus*, it was not possible to identify them to species level. Having identified the sub-fossil core sample remains, with reference to recently collected *Ectemnorhinus* weevil species in *Blepharidophyllum* mires on Marion Island to the genus level, an attempt was made to evaluate morphometric changes over time.

Both univariate and multivariate statistical analyses suggest a tendency for *Ectemnorhinus* species to decrease in morphometric size over a 4332-year period, whereas no differences were detected between core samples spanning a 1542-year time period. The question that may be posed is: What are the potential influences of these morphological changes over time? The house mouse (*Mus musculus*) was introduced on Marion Island in the late 1800s (Watkins and Cooper 1986) and is considered to be the major contributor to weevil body size reduction (Chown and Smith 1993) and a decrease in weevil population densities (Hänel and Chown 1998; Hänel 1999). With a preference for large-sized individuals (i.e., size-selective predation), mice may influence body size distributions of weevil species (Smith et al. 2002). Chown and Smith (1993) noted that various weevil species, identified as preferred prey species, decreased in body length from 1986 to 1992 on Marion Island. It is possible that similar changes in *Ectemnorhinus* species over time may have consequences for Marion Island ecosystem functioning. This is because of the important relationship that exists between body size and almost all insect life-history, physiological and ecological traits (Peters 1983; Reiss 1989; Wickman and Karlsson 1989; Harvey and Pagel 1991; Davies et al. 1999).

In addition, Marion Island mouse populations are strongly temperature-dependent and ameliorating temperatures may cause an increase in this invasive species (Smith and Steenkamp 1990; Huyser et al. 2000; Smith 2002). Crafford and Scholtz (1987) suggested that this may lead to increased weevil predation, thus decreasing overall rates of nutrient-cycling

that would exacerbate the imbalance between primary production and decomposition (Smith 1991).

Furthermore, palynological evidence (Young and Schofield 1973; Scott 1985) suggest a warming trend that began after the last glacial maximum approximately 12000 BP on Marion Island (Chown 1990). However, core peat samples studied by Scott (1985) from depths between 1.65 – 1.80 m (4140 ± 70 y BP) and between 2.80 – 2.95 m (5440 ± 310 y BP) indicated vegetation type and climate to have remained virtually unchanged during these time periods. Mire core samples from depths between 2.5 m (3910 ± 40 y BP) and 2.0 m (2641 ± 45 y BP) in the present study, represent similar time periods to those examined by Scott (1985). It may, therefore, be assumed that these core samples represent a time period of little variation in climate, which may explain the lack of morphometric change observed in head capsules sampled from 2.5 m to 2.0 m in the present study. However, significant morphometric size declines observed between sub-fossil head capsules and recently collected material may, in addition to mice predation, be attributed to climatic changes on Marion Island since the 1960s (Smith and Steenkamp 1990).

Weevil species in their various habitats on Marion Island are functioning at microclimates that closely correspond to their upper lethal temperatures (van der Merwe et al. 1997). It is, therefore, possible that temperature may have an effect on weevils from Marion Island and that a further temperature increase may have negative consequences for Marion Island weevil survival (Smith 2002). In addition, evidence from a parallel morphometric study showed four weevil species (*B. randi*, *B. parvulus*, *B. elongatus* and *P. eatoni*) to exhibit comparable morphometric size and shape changes between the mid-1960s to 2003 on both Marion and Prince Edward Islands (Chapter 4).

On the other hand, it is also possible that the results in this study may have been constrained by the small character suite used, small sample size in some instances and sampling year. These results are only based on three measurements that may have obscured the underlying morphometric pattern. In addition, the availability of only 1986 data that was collected in *Blepharidophyllum* mires for comparison with core samples may also have influenced the results in the present study. Turner (2004) reported that the end of 1986 marked the start of an El niño period, such that the potential influence of temperature on these sub-Antarctic weevils (also see Chapter 4) may be exaggerated by the inclusion of the 1986 data.

However, with an annual mean surface air temperature increase of 0.04°C on Marion Island since the late 1960s (Smith and Steenkamp 1990; Smith 1991, 2002; Weimerskirch et al. 2003), it is expected that productivity as well as nutrient demand on Marion Island will increase (Smith 1988; Smith 2002). It is therefore proposed that on-going monitoring of

weevil populations and further investigations are needed to determine factors influencing weevil populations on both Marion and Prince Edward Islands.

Acknowledgements The Directorate Antarctica and islands of the Department of Environmental Affairs and Tourism funded this work and provided logistic support at Marion Island. My sincere thanks go out to Marié Warren for her comments on the chapter. I would like to thank Prof Steven Chown for making his previously collected data available for use in the present study. I would also like to thank Mr Gert Grobler for assisting in weevil collections, Dr Dmitri Mauquoy for his assistance with the core sampling on Marion Island and Dr Stephan Woodborne based at Quadru, Environmentek in collaboration with Groningen University for the carbon-dating of weevil elytra. This material is based upon work supported by the South African National Research Foundation (NRF) in its South African National Antarctic Programme (SANAP) under Grant number GUN 2068301. Any opinions, findings and conclusions or recommendations expressed in this material are those of the author(s) and therefore the NRF does not accept any liability in regard thereto.

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“The test of success is not what you do when you are on top. Success is how high you bounce when you hit bottom”

George Patton