

On Udvardy's Insulantarctica province: a test from the weevils (Coleoptera: Curculionoidea)

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'The scattered islands of the southern, cold ocean have clear affinities with one another . . . They are the basis for my Insulantarctica province.' Udvardy, 1987, p. 190

Abstract. Analyses of the distributional patterns of weevils (Coleoptera: Curculionoidea) from several Subantarctic islands, namely, Campbell, Auckland, Snares, Antipodes, Chatham, Falklands, Tierra del Fuego, Tristan da Cunha, Inaccessible, Nightingale, Gough, Marion, Prince Edward, Crozet, Kerguelen, and Heard, as well as South America and New Zealand, were carried out in order to determine their historical relationships, and to test the validity of Udvardy's (1987) Insulantarctica province. Three parsimony analyses of endemism (PAE) considering (a) only species, (b) only supraspecific taxa, and (c) species and supraspecific taxa together, were undertaken. The following four groups emerged from the analyses: (1) New Zealand with the Snares, Auckland, Campbell, and Chatham Is., where New Zealand is the sister area to the Chatham Is., and the Auckland Is. are the sister area to Campbell I.; (2) South America with

the Falkland Is. and Tierra del Fuego, where South America and Tierra del Fuego together are the sister area to the Falkland Is.; (3) Tristan da Cunha-Gough group, with the islands following the sequence Gough, Tristan da Cunha, Inaccessible, and Nightingale Is.; and (4) Kerguelen, Heard, Crozet, Marion, and Prince Edward Is., with Kerguelen and Heard Is. being sister areas, and Marion and Prince Edward Is. together being the sister area to the Crozet Is. It is concluded that the weevil fauna does not support the existence of an Insulantarctica province; the similarities among the different Subantarctic islands are due more to similar environmental conditions rather than to a common history.

Key words. Curculionoidea, Subantarctic, biogeography, endemism.

INTRODUCTION

The Subantarctic islands, situated mostly between 48° and 55° south latitude, comprise Macquarie, Campbell, Auckland, Snares, Antipodes, Bounty, and Chatham in the South Pacific; Falklands (Malvinas), Tierra del Fuego, South Georgia, South Sandwich, and Tristan da Cunha-Gough in the South Atlantic; and Marion, Prince Edward, Crozet, Kerguelen, Amsterdam, St. Paul, and Heard in the South Indian Ocean (Fig. 1). These islands are of considerable interest because of their remarkable insect fauna, which is adapted to more rigorous conditions than the surrounding continental areas. When compared to those of tropical islands, the insect fauna is characterized by the scarcity or complete absence of several orders, namely, Hemiptera, Hymenoptera, Psocoptera, Ephemeroptera, Plecoptera, and Trichoptera (Gressitt, 1961). Within the order Coleoptera, weevils (Curculionoidea) are particularly diverse (Kuschel, 1964a, 1971, 1991), so their distributional patterns can be fruitfully investigated to ascertain the historical relationships of these islands. Weevils usually have high degrees of endemism and relatively small ranges, making them particularly useful for biogeographic analyses (Morrone, 1996a).

Although some of the Subantarctic islands are volcanic and may not have been involved in past intercontinental connections, some authors have considered that they are biogeographically interrelated. Udvardy (1987) proposed the biogeographic province of Insulantarctica (Fig. 2a), within his Antarctic realm (approximately equivalent to the Austral Kingdom; Kuschel, 1964b; Morrone, 1996b), for all the Subantarctic islands (see also Lewis-Smith, 1984; Fleming, 1987). Morrone (1992) found five generalized tracks connecting several Subantarctic islands. Chown (1994) concluded that the weevil fauna of the Kerguelen and Crozet archipelagos in the Indian Ocean were derived following vicariance with New Zealand. Other authors (Gressitt, 1961; Kuschel, 1991; Osella, 1991), however, have considered that it was better not to assume that these islands were remnants of a former larger landmass, and assigned them to different biogeographic regions (Fig. 2b).

My purpose is to examine the distributional patterns of the weevil fauna of the Subantarctic islands, in order to test these contrasting hypotheses. I examine herein the distributional patterns of the weevil taxa from these islands and other related areas, summarizing what is known about the Subantarctic weevil fauna, and then I apply the

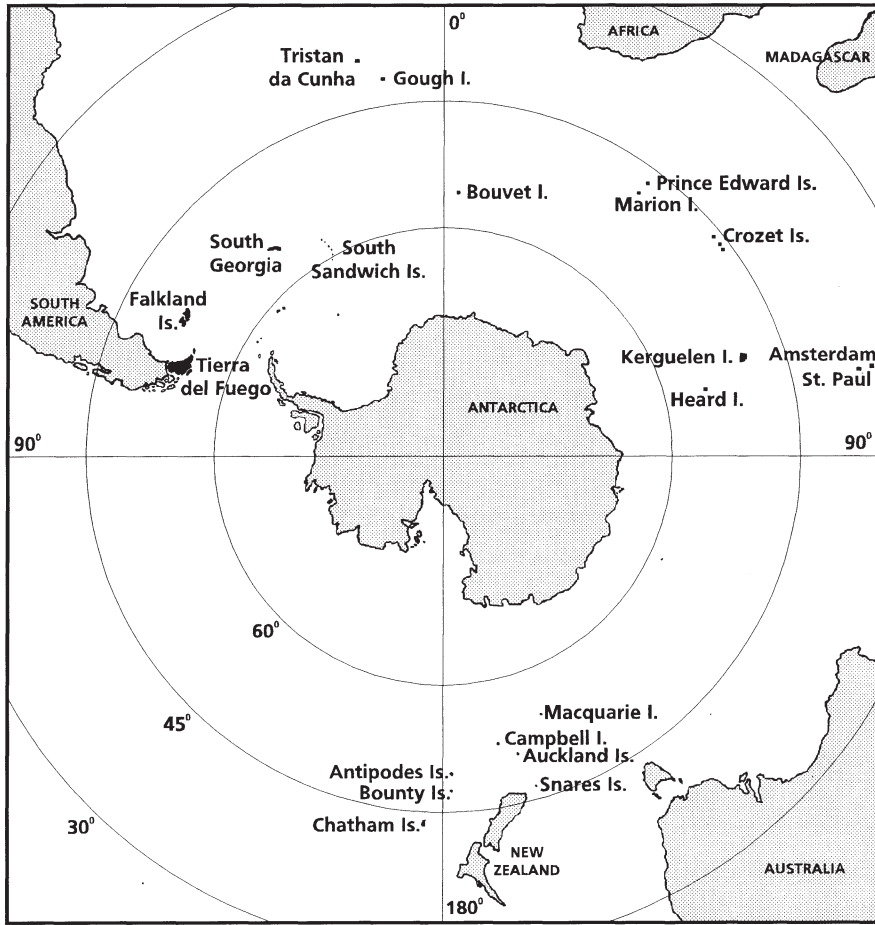


FIG. 1. Polar view of the southern hemisphere, showing the different Subantarctic islands and their closest major landmasses.

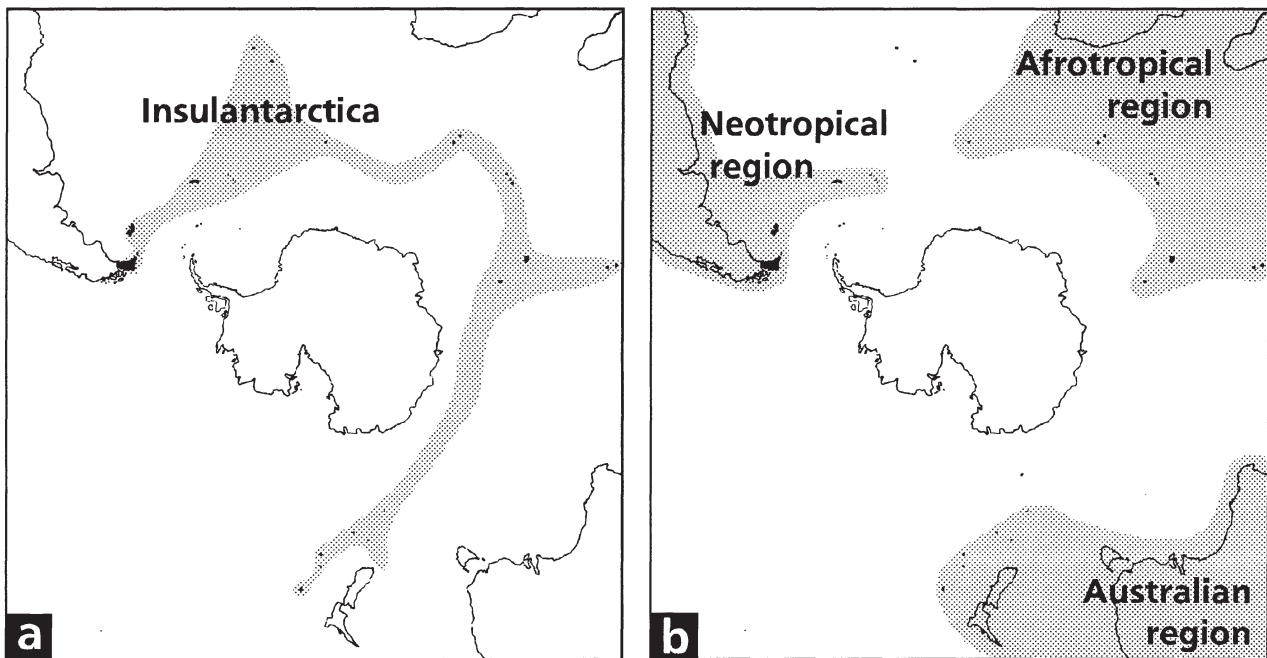


FIG. 2. Alternative hypotheses concerning the biogeographic classification of the Subantarctic islands. (a) Udvardy's (1987) Insulantarctica; (b) more traditional view.

parsimony analysis of endemism technique (Rosen, 1988) to these distributional data.

MATERIALS AND METHODS

Data were taken from several monographs, revisions, and checklists (Brinck, 1948; Kuschel, 1962, 1964a, 1971, 1991; Holloway, 1982; Wibmer & O'Brien, 1986; Voisin & Dreux, 1987; Clark & Burke, 1988; Osella, 1991; Lyal, 1993; Morrone, 1993, 1996b,c; Chown, 1994; Kuschel & Chown, 1995; Morrone & Anderson, 1995; Morrone & Roig-Juñent, 1995).

The areas of the analysis were the following Subantarctic islands (Fig. 1).

(1)-(6) Antipodes, Auckland, Bounty, Campbell, Chatham, and Snares Islands. Situated near New Zealand. The Auckland and Bounty I. are situated on the border line of the Subantarctic zone, and the Chatham Is. are sometimes not included in the group.

(7)-(11) Crozet, Heard, Kerguelen, Marion, and Prince Edward Islands. Situated in the South Indian Ocean.

(12) Falkland Islands. Situated at 52° in the South Atlantic, near South America.

(13) Tierra del Fuego. This and nearby islands represent the southernmost continental area other than Antarctica.

(14)-(17) Gough, Inaccessible, Nightingale, and Tristan da Cunha Is. Situated in the South Atlantic, these islands are outside the Subantarctic zone, but have an analogous fauna.

Some Subantarctic islands were excluded from the analyses because no data concerning weevil distributions were available, namely, South Georgia, South Sandwich, Bouvet, Amsterdam, and St. Paul. In addition, two 'external' areas were included: New Zealand and South America (Africa, the other major continental area, was not included because neither taxa inhabiting the Subantarctic islands nor their closest relatives inhabit it).

The parsimony analysis of endemism or PAE (Rosen, 1988; Cracraft, 1991; Myers, 1991) classifies areas (analogous to taxa) by their shared taxa (analogous to characters) according to the most parsimonious cladogram. PAE data consist of area × taxa matrices and the resulting cladograms represent nested sets of areas. Cladistic information is incorporated by adding supraspecific natural groups to the matrix (Morrone & Crisci, 1995).

Taxa were coded for their absence (0) or presence (1) in each area in the data matrix (Appendix 1). Taxa endemic to single areas—equivalent to autapomorphies—do not contribute with information useful for assessing relationships, and were thus not included in the matrix. Three different analyses were undertaken: (1) considering only species, (2) considering only supraspecific taxa (species groups, genera, generic groups, tribes, etc.), and (3) considering species and supraspecific taxa together. It is assumed that when no adequate samples of different geological horizons exist, data from a single time plane, but using different taxonomic levels, can provide a potential mean of corroboration (Myers, 1991).

The cladistic analyses were carried out with Hennig86

(Farris, 1988), applying the implicit enumeration (i.e. *) option. The cladograms obtained were rooted with a hypothetical area coded all zeros.

RESULTS

Distributional patterns

A total of fifty-nine weevil genera (Table 1) and 158 species have been recorded from the Subantarctic islands examined herein. (These records exclude introduced species (Kuschel, 1971; Voisin & Dreux, 1987), e.g. *Sitophilus oryzae* and *S. granarius* [Dryophthoridae], *Listronotus bonariensis* [Curculionidae: Cyclominae], and *Naupactus cervinus* [Curculionidae: Entiminae].) The Subantarctic weevil genera belong to the families Anthribidae, Eriirhinidae, and Curculionidae.

The Anthribidae comprise six genera and eleven species, all restricted to the islands of New Zealand (Holloway, 1982). *Cacephatus*, with nine species from New Zealand, Australia, New Caledonia, Lord Howe I., and Norfolk I., includes *C. aucklandicus* from the Auckland and Snares Is., and *C. propinquus*, endemic to the Chatham Is. *Lichenobius* comprises three species: *L. littoralis*, widespread on the Snares Is. and New Zealand; *L. maritimus*, endemic to the Bounty Is.; and *L. silvicola*, endemic to the Chatham Is. *Lophus* (three species) includes *L. cristatellus*, endemic to the Chatham Is., and *L. rudis*, widespread on the Chatham Is. and New Zealand. *Phymatus* (three species) includes *P. hetaera* widespread on the Chatham Is. and New Zealand. *Sharpus* (five species) includes *S. chathamensis*, endemic to the Chatham Is. *Notochoragus*, the only genus of Choraginae, has five species: three endemic to New Zealand; *N. chathamensis*, endemic to the Chatham Is.; and *N. nanus*, widespread on the Chatham Is. and New Zealand. Anthribidae are absent from the other Subantarctic islands.

The only representative of the Eriirhinidae is the genus *Bryocatus*, with *B. serripes*, endemic to the Campbell I. (Kuschel, 1964a).

The Curculionidae comprise the bulk of the weevils of the Subantarctic islands, with fifty-two genera (88%) and 146 species (92%), assigned to the subfamilies Entiminae, Cyclominae, Molytinae, Cryptorhynchinae, and Cossoninae.

The Subantarctic Entiminae include the tribes Ectemnorhinini and Entimini. The Ectemnorhinini comprise six genera and thirty-six species, all endemic to the islands of the Indian Ocean (Kuschel & Chown, 1995; references therein). *Bothrometopus* has seventeen species: *B. angusticollis* and *B. sulcatus*, endemic to Kerguelen I.; *B. crozetensis*, *B. derelictorum*, *B. desolationis*, *B. dreuxi*, *B. fasciatus*, *B. variabilis*, *B. villiersi*, *B. comes*, *B. daviesi*, and *B. gravis*, endemic to the Crozet Is.; *B. brevis* and *B. gracilipes*, widespread on Heard and Kerguelen Is.; *B. elongatus* and *B. parvulus*, widespread on Marion and Prince Edward Is.; and *B. randi*, widespread on Crozet, Marion, and Prince Edward Is. *Canonopsis* includes the single species *C. sericeus*, widespread on Heard and Kerguelen Is. *Christensenia* includes *C. antarctica* and *C. dreuxi*, endemic to the Crozet Is. *Diskar* includes the single species *D.*

TABLE 1. Distribution of the weevil genera represented in the Subantarctic islands.

Genera	Distribution
Anthribidae	
Anthribinae	
<i>Cacephatus</i>	Auckland, Chatham, Snares Is., Australia, New Caledonia and New Zealand
<i>Lichenobius</i>	Bounty, Chatham, Snares Is. and New Zealand
<i>Lophus</i>	Chatham Is. and New Zealand
<i>Phymatus</i>	Chatham Is. and New Zealand
<i>Sharpus</i>	Chatham Is. and New Zealand
Choraginae	
<i>Notochoragus</i>	Chatham Is. and New Zealand
Eririhinidae	
<i>Bryocatus</i>	Campbell I. and New Zealand
Curculionidae	
Entiminae	
Ectemnorhinini	
<i>Bothrometopus</i>	Crozet, Heard, Marion, Prince Edward and Kerguelen Is.
<i>Canonopsis</i>	Heard and Kerguelen Is.
<i>Christensenia</i>	Crozet Is.
<i>Diskar</i>	Kerguelen I.
<i>Ectemnorhinus</i>	Crozet, Heard, Kerguelen, Marion and Prince Edward Is.
<i>Palirhoeus</i>	Crozet, Kerguelen, Marion and Prince Edward Is.
Entimini	
<i>Caneorhinus</i>	Falkland Is., Tierra del Fuego, and South America
<i>Catodryobolus</i>	Auckland, Campbell Is. and New Zealand
<i>Catoptes</i>	Chatham and Snares Is. and New Zealand
<i>Cylydrorhinus</i>	Falkland Is., Tierra del Fuego and South America
<i>Heterexis</i>	Auckland and Campbell Is.
<i>Malvinus</i>	Falkland Is.
<i>Oclandius</i>	Auckland and Campbell Is.
Cyclominae	
Aterpini	
<i>Aegorhinus</i>	Tierra del Fuego and South America
<i>Alastoropolus</i>	Tierra del Fuego and South America
<i>Micropolus</i>	Tierra del Fuego and South America
Rhytirrhinini	
<i>Antarctobius</i>	Falkland Is., Tierra del Fuego and South America
<i>Falklandiellus</i>	Falkland Is., Tierra del Fuego and South America
<i>Falklandius</i>	Falkland is., Tierra del Fuego and South America
<i>Germainiellus</i>	Falkland Is., Tierra del Fuego and South America
<i>Gromilus</i>	Antipodes, Auckland, Campbell and Snares Is.
<i>Gunodes</i>	Nightingale I.
<i>Haversiella</i>	Falkland Is., Tierra del Fuego and South America
<i>Inaccodes</i>	Inaccessible I.
<i>Lanteriella</i>	Falkland Is.
<i>Listroderes</i>	Tierra del Fuego and South America
<i>Nestrius</i>	Auckland, Snares Is. and New Zealand
<i>Palaechtodes</i>	Inaccessible and Nightingale Is.
<i>Palaechtus</i>	Gough, Inaccessible, Nightingale and Tristan da Cunha Is.
<i>Puranius</i>	Falkland Is., Tierra del Fuego and South America
<i>Telurus</i>	Tierra del Fuego and South America
<i>Tristanodes</i>	Gough, Inaccessible, Nightingale and Tristan da Cunha Is.
Molytinae	
<i>Exeiratus</i>	Auckland and Snares Is.
<i>Hadramphus</i>	Snares Is. and New Zealand
<i>Notonesius</i>	Auckland Is.
<i>Phrynixus</i>	Snares Is.
Curculioninae	
Anthonomini	
<i>Anthonomus</i>	Tierra del Fuego and South America
Eugnomini	
<i>Pactolotypus</i>	Auckland, Campbell Is. and New Zealand
Tychiini	
<i>Notinus</i>	Auckland Is. and New Zealand
<i>Peristoreus</i>	Auckland, Campbell Is. and New Zealand.

continued

TABLE 1. Distribution of the weevil genera represented in the Subantarctic islands.—*continued*

Genera	Distribution
Cryptorhynchinae	
<i>Crisius</i>	Chatham Is. and New Zealand
<i>Ectopsis</i>	Chatham Is. and New Zealand
<i>Homoreda</i>	Chatham Is. and New Zealand
<i>Mecitostylus</i>	Chatham Is. and New Zealand
<i>Mesoreda</i>	Chatham Is. and New Zealand
<i>Microcryptorhynchus</i>	Auckland, Campbell, Chatham, Snares Is. and New Zealand
<i>Pachyderris</i>	Auckland, Campbell, Chatham Is. and New Zealand
<i>Patellitergum</i>	Chatham Is.
<i>Psepholax</i>	Chatham Is., New Zealand and South America
<i>Strongylopterus</i>	Chatham Is. and New Zealand
<i>Tychanopais</i>	Chatham Is. and New Zealand
Cossoninae	
Pentarthrini	
<i>Pentarthrum</i>	Auckland, Chatham, Falkland, Gough, Inaccessible, Nightingale, Snares, Tristan da Cunha Is., and New Zealand

tenuirostris, endemic to Kerguelen I. *Ectemnorhinus* has fourteen species: *E. affinis*, *E. bougainvillei*, *E. geniculatus*, *E. inexpectatus*, *E. pluricro*, *E. possessionensis*, *E. richtersi*, *E. tamarisi*, and *E. vanhoeffenianus*, endemic to the Crozet Is.; *E. drygalskii* and *E. fuscus*, endemic to Kerguelen I.; *E. marionensis* and *E. similis*, widespread on Marion and Prince Edward Is., and *E. viridis*, widespread on Heard and Kerguelen Is. The monotypic genus *Palirhoeus*, with *P. eatoni*, is widespread on the Crozet, Kerguelen, Marion, and Prince Edward Is. According to Kuschel & Chown (1995), this tribe is closely related to *Oclandius* and *Heterexis*, from the Auckland, Campbell, and Snares Is.

The Entimini have seven genera and eighteen species, distributed on the Subantarctic islands of South America and New Zealand (Kuschel, 1964a, 1971; Morrone & Roig-Juñent, 1995; references therein). *Caneorhinus* (five species) includes *C. biangulatus*, endemic to the Falkland Is., and *C. lineatus*, widespread on Tierra del Fuego and South America. The monotypic genus *Catodryobolus* includes *C. antipodus*, widespread on the Auckland and Campbell Is. (Kuschel, 1964a). *Catoptes* includes *C. brevicornis australis*, endemic to the Snares Is., and *C. b. brevicornis*, widespread on the Chatham Is. and New Zealand. *Cyldrorhinus* comprises *C. oblongus*, endemic to Tierra del Fuego; *C. lemmiscatus*, endemic to the Falkland Is.; and *C. angulatus*, *C. carinicolis*, *C. caudiculatus*, *C. fulvipes*, and *C. lateralis*, widespread on Tierra del Fuego and South America. *Heterexis* includes *H. sculptipennis*, endemic to the Auckland Is., and *H. seticostatus*, endemic to the Campbell I. (Kuschel, 1964a). Both species of *Malvinus*, *M. compressiventris* and *M. nordenskioeldi*, are endemic to the Falkland Is. *Oclandius* has three species: *O. laeviusculus*, endemic to the Auckland Is.; *O. vestitus*, endemic to the Snares Is.; and *O. cinereus*, widespread on the Auckland and Campbell Is. (Kuschel, 1964a).

The species of Cyclominae belong to the Aterpini and Rhytirrhini. Aterpini include three South American genera, each with one species on Tierra del Fuego, also occurring in the continent (Morrone, 1996c): *Aegorhinus vitulus*, *Alastoropolus strumosus*, and *Micropolus delfini*. Aterpini, although well-represented in the alpine zone of

New Zealand, are absent in the Subantarctic islands of New Zealand (Kuschel, 1971).

The Rhytirrhini are the richest Subantarctic group, with sixteen genera (27%) and fifty-two species (32%), and are represented in South America, New Zealand, and Tristan da Cunha-Gough Is. The South American genera include the endemic genera *Antarctobius*, *Falklandiellus*, *Falklandius*, *Germainiellus*, *Haversiella*, *Lanteriella*, *Listroderes*, *Puranius*, and *Telurus* (Morrone, 1993; Morrone & Roig-Juñent, 1995). *Antarctobius* has nine species: one ranged only in the continent; four endemic to the Falkland Is., *A. abditus*, *A. bidentatus*, *A. falklandicus*, and *A. vulsus*; one endemic to Tierra del Fuego, *A. yefacel*; and two widespread on Tierra del Fuego and South America, *A. germaini* and *A. hyadesii*. The monotypic genus *Falklandiellus*, with *F. suffodens*, is widespread on the Falkland Is., Tierra del Fuego, and South America. *Falklandius* has six species (Morrone & Anderson, 1995), two from southern Chile, three endemic to the Falkland Is. (*F. goliath*, *F. kuscheli*, and *F. turbificatus*), and *F. antarcticus*, widespread on the Falkland Is., Tierra del Fuego, and South America. *Germainiellus* (twelve species) includes *G. dentipennis*, *G. fulvicornis*, *G. laevirostris*, *G. lugens*, and *G. rugipennis*, widespread on Tierra del Fuego and South America, and *G. salebrosus*, endemic to the Falkland Is. *Haversiella* includes the single species *H. albolimbata*, widespread on the Falkland Is., Tierra del Fuego, and South America. Another monotypic genus, *Lanteriella*, with *L. microphthalmia*, is endemic to the Falkland Is. *Listroderes* (thirty-eight species) includes *L. delaigui*, widespread on Tierra del Fuego and South America. *Puranius* (twenty species) includes *P. championi*, *P. exsculpticollis*, and *P. scaber*, endemic to the Falkland Is., and *P. nigrinus*, widespread on Tierra del Fuego and South America. *Telurus* has two species: *T. caudiculatus*, endemic to Tierra del Fuego, and *T. dissimilis*, widespread on Tierra del Fuego and South America (Morrone & Anderson, 1995).

The two genera of Rhytirrhini from New Zealand are *Gromilus* and *Nestrius* (Kuschel, 1964a, 1971). *Gromilus*, with more than forty species, has six species and subspecies endemic to the Auckland Is. (*G. aucklandicus*, *G. cockaynei*,

G. fallai, *G. insularis insularis*, *G. narinusos*, and *G. veneris veneris*), three endemic to the Campbell I. (*G. exiguus*, *G. insularis robustus*, and *G. veneris setarius*), one endemic to the Snares (*G. laqueorum*), and one endemic to the Antipodes Is. (*G. insularis antipodarum*). *Nestrius*, with twenty-seven species, includes *N. laqueorum*, endemic to the Snares Is., and *N. bifurcus*, widespread on the Auckland Is. and New Zealand.

The Rhytirrhini from Tristan da Cunha-Gough include four monotypic genera (*Gunodes*, *Inaccodes*, *Palaechtodes*, and *Palaechtus*) and *Tristanodes*, all endemic to these islands (Brinck, 1948; Kuschel, 1962; Osella, 1991). *Gunodes major* and *Palaechtus glabratus* are endemic to Nightingale I. *Inaccodes oblongus* is endemic to Inaccessible I. *Palaechtodes cossonoides* is widespread on Inaccessible and Nightingale Is. The eleven species of *Tristanodes* were classified in four species groups (Brinck, 1948). The *T. attai* species group includes *T. attai* from Tristan da Cunha, *T. medius* from Inaccessible I., and *T. minor* from Nightingale I. The *T. craterophilus* species group includes *T. craterophilus* from Tristan da Cunha, *T. echinatus* from Inaccessible I., and *T. insolidus* from Nightingale I. The *T. integer* species group includes *T. integer* from Inaccessible I. and *T. sivertseni* from Nightingale I. The *T. reppetonis* species group includes *T. conicus* and *T. reppetonis* from Inaccessible I. and *T. scirpophilus* from Gough and Tristan da Cunha I. These genera are closely related to the American genus *Listronotus* (Morrone, 1994).

The Molytinae have four genera, restricted to the Subantarctic islands of New Zealand. *Exeiratus*, which has four species endemic to New Zealand and its Subantarctic islands, includes *E. laqueorum*, endemic to the Snares Is., and *E. turbotti*, endemic to the Auckland Is. (Kuschel, 1964a, 1971). *Hadramphus* comprises four species (Robin Craw, personal communication), of which *H. spinipennis* is endemic to the Chatham Is., and *H. stilbocarpae* is widespread on the Snares Is. and New Zealand. *Notonesius aucklandicus* is endemic to the Auckland Is. *Phrynixus* has numerous species in New Zealand, with *P. laqueorum* endemic to the Snares Is. (Kuschel, 1964a).

The species of Curculioninae are assigned to the tribes Anthonomini, Eugnomini, and Tychiini. The Anthonomini include *Anthonomus ornatus* and *A. signatipennis*, widespread on Tierra del Fuego and South America (Clark & Burke, 1988). The Eugnomini include the genus *Pactolotypus*, with *P. depressirostris*, widespread on the Auckland Is. and New Zealand, and *P. subantarcticus*, widespread on the Auckland Is., Campbell I., and New Zealand (Kuschel, 1964a). The Tychiini include *Notinus cordipennis aucklandicus* from Auckland Is. and New Zealand, and *Peristoreus innocens*, from the Auckland Is., Campbell I. and New Zealand.

The Cryptorhynchinae include eleven genera from New Zealand and its Subantarctic islands (Kuschel, 1964a; Lyal, 1993): *Crisius*, *Ectopsis*, *Homoreda*, *Mecitostylus*, *Mesoreda*, *Microcryptorhynchus*, *Pachyderris*, *Patellitergum*, *Psepholax*, *Strongylopterus*, and *Tychanopais*. *Crisius* has two species: *C. lineirostris*, endemic to the Chatham Is., and *C. subcarinatus*, widespread on the Chatham Is. and New Zealand. *Ectopsis ferrugalis*, *Mesoreda sulcifrons*, and

Mecitostylus douei are all widespread on the Chatham Is. and New Zealand. *Homoreda* includes two species: *H. flavisetosa*, endemic to the Chatham Is., and *H. murina*, widespread on the Chatham Is. and New Zealand. *Microcryptorhynchus* includes *M. ferrugo*, endemic to the Auckland Is.; *P. squamiventris*, endemic to the Chatham Is.; *M. latitarsus*, widespread on the Auckland Is. and New Zealand; *M. kronei*, *M. multisetosus*, and *M. piciventris*, widespread on the Auckland Is., Campbell I., and New Zealand; *M. planidorsis*, widespread on the Auckland Is., Campbell I., Snares Is., and New Zealand; and *M. suillus*, widespread on the Auckland, Campbell, and Chatham Is., and New Zealand. *Pachyderris* has four species, one of which, *P. punctiventris*, is widespread on the Auckland and Campbell Is., and New Zealand. *Patellitergum rectirostre* is endemic to the Chatham Is. *Psepholax* includes *P. coronatus*, *P. crassirostris*, and *P. sulcatus*, widespread on the Chatham Is. and New Zealand. *Strongylopterus* includes *S. chathamensis*, endemic to the Chatham Is., and *S. hylobioides*, widespread on the Chatham Is. and New Zealand. *Tychanopais fougeri* is widespread on the Chatham Is. and New Zealand.

The Subantarctic Cossoninae include only the genus *Pentarthrum*, which ranges widely in New Zealand, New Caledonia, Tasmania, Juan Fernandez Is., southern Chile, the Falklands, and Tristan da Cunha-Gough Is. It includes *P. carmichaeli*, widespread on the Falklands, Gough, Inaccessible, Nightingale, and Tristan da Cunha Is., and New Zealand; and *P. spadiceum*, widespread on the Auckland, Chatham, Snares Is., and New Zealand (Kuschel, 1964a, 1991).

Parsimony analysis of endemism

PAE considering only species yielded two single most parsimonious cladograms, with seventy-two steps, consistency index of 0.72, and retention index of 0.74 (consensus cladogram in Fig. 3a). The analysis considering only supraspecific taxa yielded twenty-five single most parsimonious cladograms, with seventy-nine steps, consistency index of 0.69, and retention index of 0.78 (consensus cladogram in Fig. 3b). When species and supraspecific taxa were combined, PAE yielded twelve single most parsimonious cladograms, with 152 steps, consistency index of 0.69, and retention index of 0.75 (consensus cladogram in Fig. 3c). Comparison of the cladograms obtained in the three analyses reveals the following four groups of island and 'external' areas.

- (1) New Zealand with the Snares, Auckland, Campbell, and Chatham Is., where New Zealand is the sister area to the Chatham Is., and the Auckland Is. are the sister area to Campbell I.
- (2) South America with the Falkland Is. and Tierra del Fuego, where South America and Tierra del Fuego together are the sister area to the Falkland Is.
- (3) Tristan da Cunha-Gough group, with the islands following the sequence Gough, Tristan da Cunha, Inaccessible, and Nightingale Is.
- (4) Kerguelen, Heard, Crozet, Marion, and Prince Edward Is., with Kerguelen and Heard Is. being sister areas,

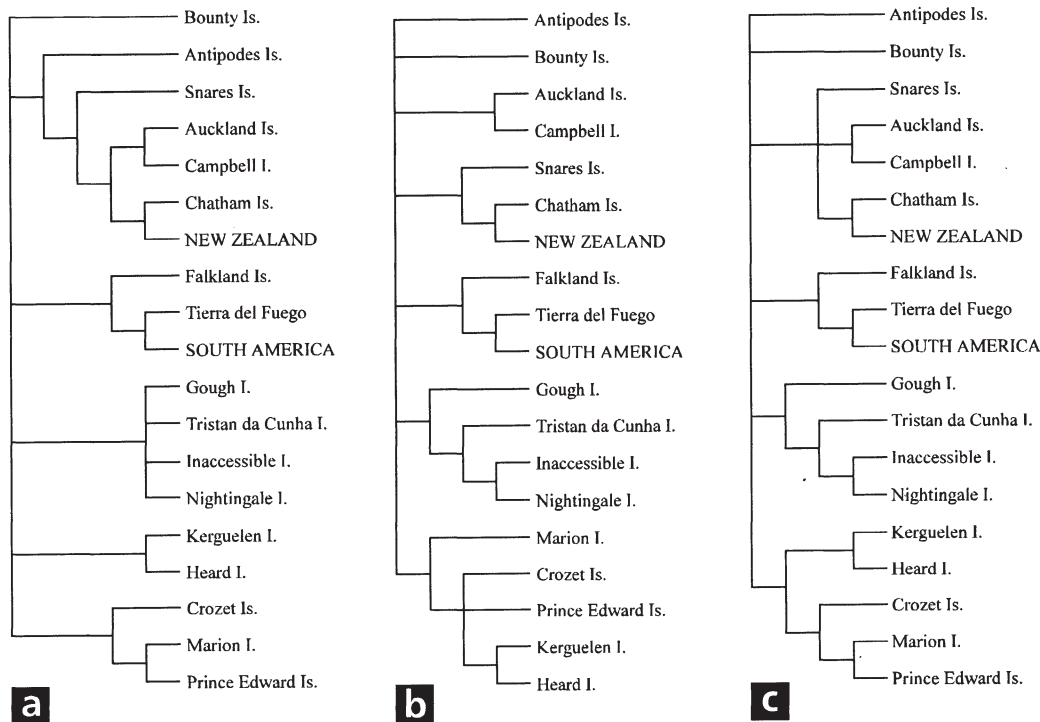


FIG. 3. Consensus cladograms obtained by PAE, depicting the relationships of the Subantarctic islands, New Zealand, and South America. (a) analysis 1 (species); (b) analysis 2 (supraspecific taxa); (c), analysis 3 (species and supraspecific taxa together).

and Marion and Prince Edward Is. together being the sister area to Crozet Is.

DISCUSSION

These results contrast with Udvardy's (1987) Insulantarctica province (Fig. 2a), and partially coincide with Lewis-Smith (1984), who considered closer relationships of some Subantarctic islands with New Zealand and others with South America (Fig. 2b). Although these areas are now widely separated, they shared a common biota in the Mesozoic. Their later separation led to *in situ* differentiation, and with different islands being adjacent to different continental areas, they received various immigrants during the Tertiary that gave them their particular character (Fleming, 1987). The great conformity of the results of the three PAE analyses of weevil distributions (which are based on different hierarchical levels and thus may provide some temporal dimension) indicates that these islands should have been stable for a long period. It is hypothesized that some of the features that led authors to postulate relationships among the Subantarctic islands are of ecological nature, due to similar environmental conditions, rather than to a common history.

Tristan da Cunha-Gough and the South Indian Ocean Is., although conforming cohesive groups in the analyses, do not seem to be related to any other area. It has been postulated that the weevil fauna of the Tristan da Cunha-Gough islands is related to that from South America (Kuschel, 1962; Osella, 1991). Chown (1994) reviewed the evolution and biogeography of the Ectemnorhini from

the South Indian Ocean islands, concluding that they were derived following vicariance with New Zealand, via eastern Antarctica (Brundin, 1988 has argued the same in relation to Chironomid midges). Although in some of the cladograms obtained, the Tristan da Cunha-Gough and the South Indian Ocean Is. were grouped together with New Zealand Subantarctic islands, I find this evidence not totally supporting their relationships.

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APPENDIX 1. Data matrix for analysis 3 (combining species and supraspecific taxa). Analyses 1 and 2 were undertaken excluding the non relevant columns.

root	000000000	000000000	000000000	000000000	000000000	000000000
Antipodes Is.	000000000	000000000	000000000	000000000	000000000	000110000
Auckland Is.	110000000	010000000	000000110	000001110	000000000	0001110001
Bounty Is.	001000000	000000000	000000000	000000000	000000000	0000000000
Campbell Is.	000000000	110000000	000000110	000001110	000000000	0001110000
Chatham Is.	101011111	000000000	000000001	000000000	000000000	0000000000
Snares Is.	111100000	010000000	000000001	000000100	000000000	0001000001
Crozet Is.	000000000	011100010	100010000	000000000	000000000	0000000000
Heard I.	000000000	0111101001	100100000	000000000	000000000	0000000000
Kerguelen I.	000000000	0111101001	100110000	000000000	000000000	0000000000
Marion I.	000000000	0110010110	111010000	000000000	000000000	0000000000
P. Edward I.	000000000	0111010110	111010000	000000000	000000000	0000000000
Falkland Is.	000000000	000000000	000001000	100000000	0000111100	0000001000
T. del Fuego	000000000	000000000	0000110001	1111100011	1111111111	1100011100
Gough I.	000000000	000000000	000000000	000000000	000000000	0000000000
Inaccessible I.	000000000	000000000	000000000	000000000	000000000	0000000000
Nightingale I.	000000000	000000000	000000000	000000000	000000000	0000000000
T. da Cunha	000000000	000000000	000000000	000000000	000000000	0000000000
New Zealand	101111111	100000000	0000000101	000000000	000000000	00001000001
S. America	000000000	000000000	0000011000	1111110001	1111111111	1110001110

APPENDIX 1—continued

root	000000000	000000000	000000000	000000000	000000
Antipodes Is.	000000000	000000000	000000000	000000000	000000
Auckland Is.	100000000	000011111	000000111	111110000	001101
Bounty Is.	000000000	000000000	000000000	000000000	000000
Campbell Is.	000000000	000010010	000000110	111110000	000000
Chatham Is.	000000000	010000000	111111000	001101111	110101
Snares Is.	000000000	010000000	000000100	010000000	001101
Crozet Is.	000000000	000000000	000000000	000000000	000000
Heard I.	000000000	000000000	000000000	000000000	000000
Kerguelen I.	000000000	000000000	000000000	000000000	000000
Marion I.	000000000	000000000	000000000	000000000	000000
P. Edward I.	000000000	000000000	000000000	000000000	000000
Falkland Is.	000000001	000000000	000000000	000000000	000110
T. del Fuego	000000011	101000000	000000000	000000000	000000
Gough I.	010100010	000000000	000000000	000000000	000110
Inaccessible I.	011111100	000000000	000000000	000000000	000110
Nightingale I.	011111100	000000000	000000000	000000000	000110
T. da Cunha	010110100	000000000	000000000	000000000	000110
New Zealand	100000000	010011111	111111111	111111111	110111
S. America	010000011	101100000	000000000	000001001	000100

Taxa (columns): 1, *Cacephatus*; 2, *C. aucklandicus*; 3, *Lichenobius*; 4, *L. littoralis*; 5, *Lophus*; 6, *L. rudis*; 7, *Phymatus hetaera*; 8, *Sharpus*; 9, *Notochoragus*; 10, *N. nanus*; 11, *Bryocarus*; 12, *Oclandius-Heterexis-Ectemnorhinini*; 13, *Ectemnorhinini*; 14, *Bothrometopus*; 15, *B. brevis*; 16, *B. elongatus*; 17, *B. gracilipes*; 18, *B. parvulus*; 19, *B. randi*; 20, *Canonopsis*; 21, *Ectemnorhinus*; 22, *E. marioni*; 23, *E. similis*; 24, *E. viridis*; 25, *Palirhoeus*; 26, *Caneorhinus*; 27, *C. lineatus*; 28, *Catodryobolus*; 29, *C. antipodus*; 30, *Catoptes*; 31, *Cylydrorhinus*; 32, *C. angulatus*; 33, *C. carinacollis*; 34, *C. caudiculatus*; 35, *C. fulvipes*; 36, *C. lateralis*; 37, *Heterexis*; 38, *Oclandius*; 39, *O. cinereus*; 40, *Aegorhinus*; 41, *Alastoropolus*; 42, *Micropolus*; 43, *Antarctobius*; 44, *A. germani*; 45, *A. hyadesii*; 46, *Falklandiellus*; 47, *Falklandius*; 48, *F. antarcticus*; 49, *Germaniellus*; 50, *G. fulvicornis*; 51, *G. dentipennis*; 52, *G. laevirostris*; 53, *G. lugens*; 54, *G. rugipennis*; 55, *Gromilus*; 56, *G. insularis*; 57, *G. veneris*; 58, *Haversiella*; 59, *Listroderes*; 60, *L. delaigui*; 61, *Nestrius*; 62, *N. bifurcus*; 63, *Listronotus* generic group; 64, *Palaechtodes*; 65, *Tristanodes*; 66, *T. attai* species group; 67, *T. craterophilus* species group; 68, *T. integer* species group; 69, *T. reppetoni* species group; 70, *Puranius*; 71, *P. nigrinus*; 72, *Telurus*; 73, *Hadramphus*; 74, *Anthonomus ornatus*; 75, *A. signatipennis*; 76, *Pactolotypus*; 77, *P. depressirostris*; 78, *P. subantarcticus*; 79, *Notinus*; 80, *Peristoreus*; 81, *Crisius*; 82, *Ectopsis*; 83, *Homoreda*; 84, *H. murina*; 85, *Mecistostylys*; 86, *Mesoreda*; 87, *Microcryptorhynchus*; 88, *M. kronei*; 89, *M. latitarsis*; 90, *M. multisetosus*; 91, *M. piciventris*; 92, *M. planidorsis*; 93, *M. suillus*; 94, *Pachyderris*; 95, *P. punctiventris*; 96, *Psepholax*; 97, *P. coronatus*; 98, *P. crassirostris*; 99, *P. sulcatus*; 100, *Strongylopterus*; 101, *S. hylobioides*; 102, *Tychanopais*; 103, *Exeiratus*; 104, *Pentarthrum*; 105, *P. carmichaeli*; 106, *P. spadiceum*.