

Biogeography and Evolution of New Zealand Priasilphidae (Coleoptera: Cucujoidea)

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Abstract

The phylogenetic relationships of the seven species of the endemic New Zealand genus *Priasilpha* were reconstructed by a cladistic analysis of 22 adult characters. One fully resolved tree was produced that was rooted with the Tasmanian species *Priastichus megathorax* with the following relationships among *Priasilpha* (distributions in square brackets): (*P. aucklandicus* [Auckland Island] + *P. obscura* [South Island and southern North Island]) (*P. angulata* [Franz Joseph Glacier, Westland] (*P. earlyi* [Kellys Creek, Arthurs Pass] (*P. carinata* [Mt. Arthur, Northwest Nelson] (*P. bufonia* [Richmond Range, Northwest Nelson, Marlborough] + *P. embersoni* [Paparoa Range, Buller Region])))). The only winged species, *P. obscura*, is placed as a sister taxon to *P. aucklandicus*, both of which are in a basal clade that is a sister group to the remaining species. Aptery evolved early in the genus and there is a statistically significant morphological trend towards body roundness, with basal species elongate in shape and derived species progressively more rounded. The *P. angulata* clade is found to the west of the Alpine Fault and is part of the Challenger Plateau, a cratonic fragment forming the southernmost limit of the Melanesian Rift. *Priasilpha obscura* is found mainly on Torlesse and Waipapa terranes and is of east Gondwanan origin. *Priasilpha aucklandicus* is restricted to the Campbell Plateau, a cratonic fragment derived from west Gondwana. The phylogeny of *Priasilpha* suggests that the Melanesian Rift-Torlesse split occurred prior to the East-West Gondwanan split (hypothesis 1), which is clearly contradicted by their relative ages. If the flighted *P. obscura* is deleted from consideration or if it is assumed that it was once a Campbell Plateau species, then this older distribution supports a hypothesis that there is a basal East-West Gondwanan split occurring about

100 Ma. If, however, *P. aucklandicus* evolved from a *P. obscura* + *P. aucklandicus* ancestor some time after 20 Ma, then the derived east-west Gondwanan split is falsified and the distributions are an artefact due to faunal mixing (hypothesis 2). Examination of a 3-taxon statement for the genera of Priasilphidae (*Chileosilpha* [Southern Chile] (*Priastichus* [Tasmania] + *Priasilpha* [New Zealand])) supports hypothesis 2 where the East-West Gondwana split preceded one between East Gondwana and the Melanesian Rift.

Keywords: Cucujoidea; Biogeography; Alpine fault; wing loss

Introduction

When New Zealand separated from Gondwana it carried with it some of the world's oldest lineages, a few of which are still thriving in the country's intact habitats. Some New Zealand relicts are famous, like ratite birds, and are well documented and researched; others, in fact most of them, are obscure, unstudied, and have yet to be added to the "Biogeographers' Almanac." Among New Zealand's diverse beetle fauna consisting of approximately 10,000 species (Leschen *et al.* 2003), there are numerous examples of Gondwanan relicts and included among them is the family Priasilphidae (Leschen *et al.* 2005). The family Priasilphidae, originally proposed as a subfamily of Phloeostichidae (Sen Gupta and Crowson 1969), now contains 11 species in three genera distributed in southern Chile (*Chileosilpha* Leschen, Lawrence, and Ślipiński: 1 sp.), Tasmania (*Priastichus* Crowson: 3 spp.), and New Zealand (*Priasilpha* Broun: 7 spp.) (Leschen *et al.* 2005). Members of *Priasilpha* are forest dwelling and feed mainly on fungal spores, including those of sooty moulds. Fungal spores are often found in waxy

Table 1. Priasilpha species and their distribution in New Zealand (Leschen et al. 2005).

Species	Distribution
<i>P. angulata</i> Leschen, Lawrence, & Ślipiński	Westland near Franz Joseph and Fox Glaciers
<i>P. aucklandicus</i> Leschen, Lawrence, & Ślipiński	Auckland Islands
<i>P. bufonia</i> Leschen, Lawrence, & Ślipiński	Richmond Range, Marlborough ¹
<i>P. carinata</i> Leschen, Lawrence, & Ślipiński	Northwest Nelson
<i>P. earlyi</i> Leschen, Lawrence, & Ślipiński	Kellys Creek, Arthurs Pass NP
<i>P. embersoni</i> Leschen, Lawrence, & Ślipiński	Paparoa Range, Buller Region
<i>P. obscura</i> Broun	South Island and southern North Island

¹The Marlborough distribution is a new record for *P. bufonia*: 3 specimens, NEW ZEALAND, SD, Opouri Saddle, Bridle Tk, 8 Apr 2004, R. Leschen, H. Harman, litter RL858, 41°08'S, 17°443'E

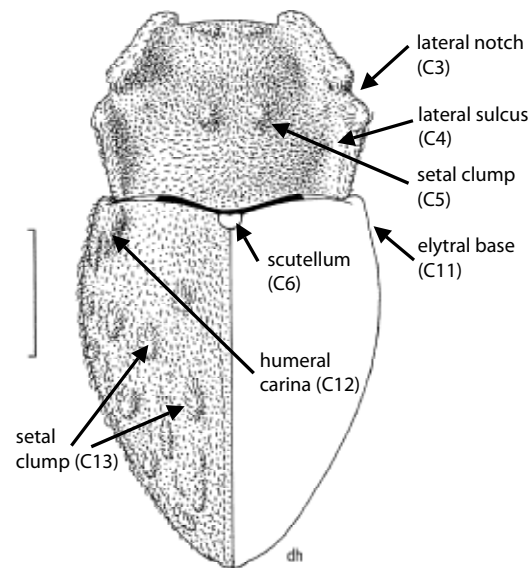


Fig. 1. Dorsal habitus of *Priasilpha angulata* with some characters indicated that were used in the cladistic analysis (numbers correspond to those in Appendix 1). (Scale bar = 1 mm).

secretions on their bodies (see the review of the species by Leschen *et al.* 2005). Now that species names are available and a phylogeny exists for the genera (and its relatives in Cucujoidea), we take this opportunity to reconstruct the relationships of the New Zealand endemic genus *Priasilpha* and determine its history in New Zealand.

The New Zealand species of *Priasilpha* (Table 1) range in the south from the Auckland Islands

(Adams Island) on the subantarctic Campbell Plateau to about the middle of the North Island. Apart from *P. obscura* Broun, which is widespread and found from Stewart Island to the North Island and is the only winged species, all members have geographic distributions that are restricted, and are often known from a handful specimens from nearby locations. In addition to restricted distributions that appear to be related to geology, the species of *Priasilpha* have divergent body forms ranging from being broadly elongate (*P. angulata*, *P. aucklandicus* and *P. obscura*) to ovate (*P. carinata* and *P. earlyi*) to strongly rounded (*P. bufonia* and *P. embersoni*). How did the distribution of *Priasilpha* come about and is there a phylogenetic pattern to the differences in body shape? This paper attempts to answer these questions.

Materials and Methods

Phylogenetic and Morphometric Analyses

We scored 22 characters from adult morphology (see Fig. 1 and Appendix 1) and data were coded and entered into MacClade version 3 (Maddison & Maddison 1992) and analysed using PAUP* Version 4.0b8 (Swofford 2003). The data matrix is shown in Table 2. The settings used in PAUP* were for the most part the default options for the software including heuristic tree searches with 100 random addition sequence replicates with steepest descent option; character states were treated as unordered. Branch support was determined by Bremer support (Bremer 1988), which measures the number of steps a clade will lose as tree length

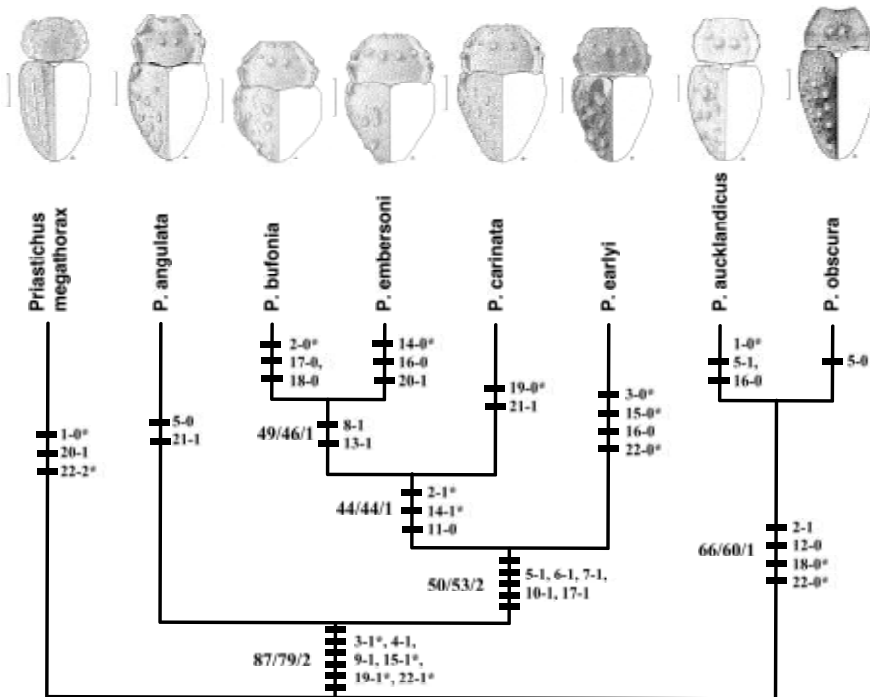


Fig. 2. Phylogeny of *Priasilpha* spp. rooted with *Priastichus megathorax*. Support values are shown to the left of the branches nodes (Bootstrap/Jackknife/Decay values) while characters are optimised to the right (* are characters that are supported by ACCTRAN, otherwise these are unambiguous). (Scale bars = 1 mm).

is increased, using Autodecay 3.0 (Ericksson & Wikström 1995) and by bootstrap (Felsenstein 1985; Sanderson 1995) and jackknife analyses (see Farris *et al.* 1995) with 100 replications each with simple addition sequences. Tree rooting and polarity of character states was determined by including the priasilphid species *Priastichus megathorax* Leschen, Lawrence, and Ślipiński in the data matrix as an outgroup. Ambiguous characters were optimised using ACCTRAN optimisation (Maddison *et al.* 1984).

Significant trends in the differences in body shape were determined by simple linear regression between body shape and cladogram node (see methods in Leibherr 1988). Cladogram node was numbered from the base to the apex. Overall body shape was calculated as a ratio of body length (from the anterior edge of the pronotum to the apex of the elytron) to greatest elytral width. The numbers of specimens measured and mean ratios are provided in Fig. 4 while additional information about characters is presented in Leschen *et al.* (2005).

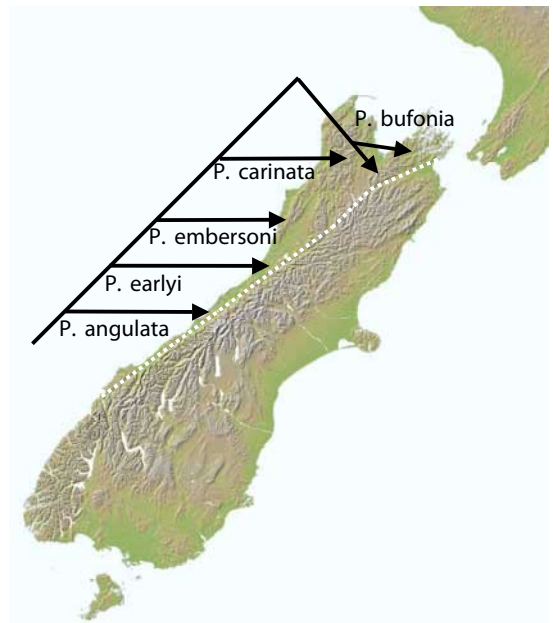


Fig. 3. Distribution of *Priasilpha angulata* clade in New Zealand. The dashed line indicates the Alpine Fault. (Map modified after <http://www.geographx.co.nz/>).

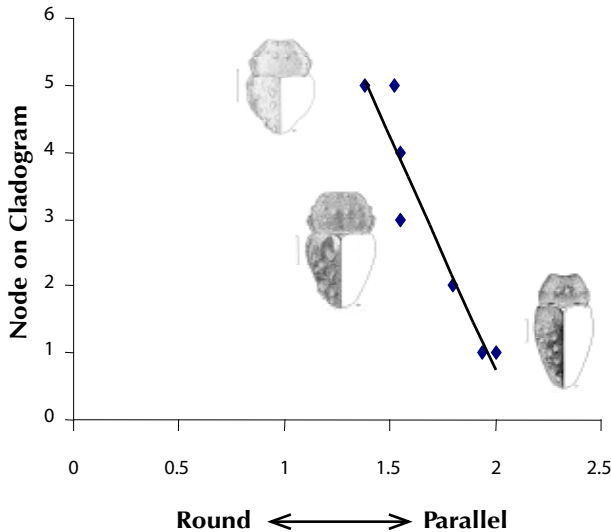


Fig. 4. Regression line showing relationship of body shape as indicated by the elongateness (x-axis) to cladogram node (y-axis). $y = -6.9814x + 14.709$. Ratios are as follows: *P. angulata* (1.8, n = 10), *P. aucklandicus* (2.0, n = 1), *P. bufonia* (1.38, n = 7), *P. carinata* (1.55, n = 6), *P. earlyi* (1.55, n = 3), *P. embersoni* (1.52, n = 2), *P. obscura* (1.94, n = 10).

Results

One tree resulted from the cladistic analysis (tree length = 46, consistency index = 0.65, retention index = 0.61) and is shown in Fig. 2. *Priasilpha aucklandicus* and *P. obscura* are grouped as sister taxa, and are in turn a sister taxon to the rest of *Priasilpha*, which we call the *P. angulata* clade. These basal nodes were in general well supported by Bootstrap and Jackknife analyses whereas decay values were very poor, probably due to the relatively small number of supportive characters per node. The remaining nodes are poorly supported, though the node above *P. angulata* is supported by two unambiguous character changes. Though portions of the tree are poorly supported, the analysis is based on homologies recognised through the careful study of microstructure and external morphology and is sufficient for reconstructing the relationships of a monophyletic group in the context of a cladistic parsimony analysis (Farris 1983) and for examining the evolution of the group. Future tests of the phylogenetic relationships we propose could be evaluated based on additional character systems (e.g., larval and behaviour).

Nodes were numbered from 1-5 starting at the base of *Priasilpha*. Based on the nodal sequence

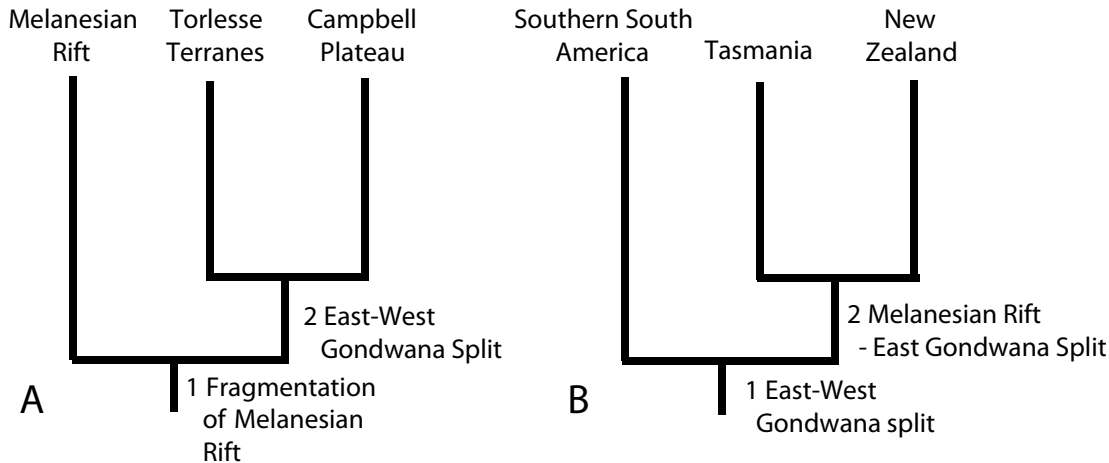


Fig. 5. Area relationships implied by the cladogram of *Priasilpha* and *Priastichus* (A) and on all three genera of Priasilphidae (B).

there was a significant relationship between body shape and distance from the root ($R^2 = 0.9037$; $P = 0.007$; Fig. 4) where the basal species are elongate and apical species are more ovate.

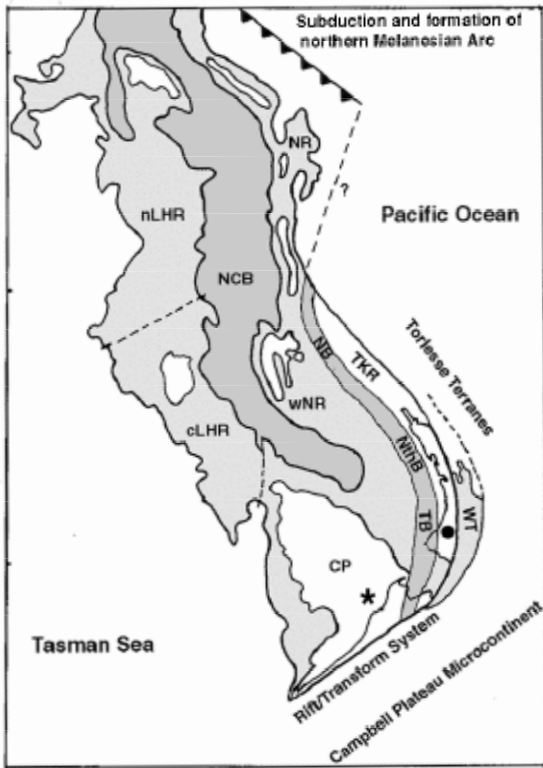


Fig. 6. Diagrammatic representation of the Melanesian Rift at circa 40 Ma with dark grey shading indicating intra-rift systems and light grey indicating depths of 500m-3000m. CP = Challenger Plateau, cLHR = central Lord Howe Rise, nLHR = northern Lord Howe Rise, NCB = New Caledonia Basin, NB = Norfolk Basin, NR = Norfolk Ridge, wNR = western Norfolk Ridge, NthB = Northland Basin, TB = Taranaki Basin, TKR = Three Kings Rise, wNR = western Norfolk Ridge, WT = Waipapa terrane. Star = ancestor of *P. angulata* clade, closed circle = ancestor of *P. aucklandicus* + *P. obscura* clade.

Discussion

Biogeography

Distributions of *Priasilpha* are shown in Table 1. *Priasilpha obscura*, the only winged New Zealand species, is widely distributed throughout the South Island and southern North Island. Its distribution is largely east of the Alpine Fault in the South Island, though there are records of the species in Buller, Westland, and Northwest Nelson (Leschen *et al.* 2005). The distribution of this species is predominantly on greywakes of the Torlesse and Waipapa terranes, both of which are of East Gondwana origin (Adams *et al.* 1998). *Priasilpha aucklandicus* is restricted to the *Metrosideros* forests of Adams Island located in the southern sector of the Auckland Island archipelago situated on the west Gondwanan Campbell Plateau microcontinent. The remaining species, which we call the *P. angulata* clade, are distributed to the west of the Alpine Fault (see Fig. 3) on the southern part of the Lord Howe Rise known as the Challenger Plateau. This plateau is composed of continental crust derived from the east Gondwanan craton, and is part of the Australian Plate.

A simplified area cladogram, produced by replacing species names with geological units as areas, is shown in Fig. 5a. Nodes 1 and 2 in Fig. 5a are labelled with the splitting events implied by the area cladogram. Michaux & Leschen (2005) date node 2 to circa 100 Ma, while node 1 is unlikely to be older than 40 Ma, and probably younger. Fig. 6 shows our reconstruction of the Melanesian rift at circa 40 Ma in the Eocene. At this time spreading in the Tasman Sea had finished (Gaina *et al.*, 1998) and the propagation of the Pacific/Australian plate boundary into the southern section of the Melanesian Rift had yet to begin. Subduction and the formation of related arc volcanics of the Melanesian arc were at the time restricted to the northern part of the Melanesian Rift (Coleman 1997). At 40 Ma much of the Melanesian Rift would have subsided due to thermal relaxation and crustal thinning. In Fig. 6 we have schematically indicated the extent of possible land/shallow marine environments as unshaded areas. These are mostly restricted to southern and eastern areas of the Melanesian Rift (the Challenger Plateau/west coast South Island and Norfolk Ridge/western North Island respectively).

Two rift systems are indicated in Fig. 6. The New Caledonia Basin was an old, pre-break up feature that had subsided to bathyl depths by 60 Ma (Stagpoole *et al.* 2000). The second rift feature consists of a series of basins along the western margin of the North Island and Three Kings Rise (Kamp 1986; King 2000). We relate the isolation of the Challenger Plateau from western North Island/Three Kings Rise by subsidence of the southern portion of this rift system during the Eocene to the basal node in Fig. 5a, with the ancestor of the *P. angulata* clade restricted to the Challenger Plateau and the ancestor of *P. obscura* + *P. aucklandicus* restricted to the western North Island segment of the Melanesian Rift. However, there is clearly a problem with a younger date preceding the older date. We suggest two hypotheses that relate to the distributions of sister taxa *P. obscura* and *P. aucklandicus* as follows.

Hypothesis 1: Relicts of the Campbell Plateau

Widespread species, such as *P. obscura*, have long posed a problem for biogeographic analysis. Widespread species are analogous to primitive characters in a phylogenetic analysis leading to problems analogous to polyphyly and paralogy. Various solutions have been suggested (see for example Van Veller *et al.* 2003), but paralogy remains problematic for constructing interpretable general area cladograms (Nelson & Ladiges 1996). One solution is to ignore widespread species at some stage of the analysis. Removing the widespread species *P. obscura* from the analysis would collapse node 2 and make node 1 a basal East-West Gondwana split (Fig. 5a).

A similar result follows from reassigning *P. obscura* as a Campbell Plateau species. This assignment is justified by regarding its distribution on the Campbell Plateau microcontinent as part of its original (primitive) distribution (Michaux & Leschen 2005), and its distribution elsewhere as derived, a result of mixing west and east Gondwanan faunas at circa 20 Ma (Michaux & Leschen 2005). Hypothesis 1 would imply that *P. aucklandicus* is a west gondwanan relict.

Hypothesis 2: Faunal Mixing

Priasilpha aucklandicus may be a relatively recently derived species that evolved from its ancestor

sometime after 20 Ma when the west gondwanan Campbell Plateau amalgamated with the southern part of the Melanesian Rift-Arc complex (Michaux & Leschen 2005). This hypothesis implies that node 2 in Fig. 5a is an artefact of faunal mixing and that the basal split between the Melanesian Rift and Melanesian Arc is correctly assigned to node 1 in Fig. 5a.

Choosing Between Hypotheses

Hypothesis 1 predicts *P. aucklandicus* has been isolated from all other mainland New Zealand species for perhaps 100 My when distinct east and west Gondwanan beetle faunas first evolved (Michaux & Leschen 2005). Appropriate character data, for example sequence data for genes that have undergone moderate mutation rates, should give a long branch distance between *P. aucklandicus* + *P. obscura* and the *P. angulata* clade (Fig. 2). There may or may not be a large genetic distance between *P. aucklandicus* and *P. obscura*, depending on the time of separation of these two species during their isolation on the Campbell Plateau, and the subsequent local extinction on the Campbell Plateau of *P. obscura*.

Hypothesis 2, by contrast, predicts isolation of *P. aucklandicus* from *P. obscura* no earlier than 20 Ma following amalgamation of the Campbell Plateau with the rest of New Zealand and spread of *P. obscura* southwards. While calculation of some genetic distance measure between *Priasilpha* species has the potential to distinguish between these competing hypotheses, these methods and their interpretation are not without their problems (e.g., Arbogast *et al.* 2002), and in any case, the data are not available and requires fresh material for DNA extraction for all species. However, additional phylogenetic data also have the potential to distinguish between hypotheses 1 and 2.

Fig. 5b shows the area cladogram derived from the phylogeny of the genera of Priasilphidae, a 3-taxon statement that is (*Chileosilpha* (*Priastichus* + *Priasilpha*)) according to Leschen *et al.* (2005) and adds two further nodes to the base of the *Priasilpha* tree (Fig. 2). *Priastichus* species are flightless species restricted to Tasmania, while *Chileosilpha* is a flight-capable monotypic genus restricted to Chile. In this more inclusive study, the separation of east and west Gondwana is basal, followed by separation of the Melanesian Rift from

east Gondwana. The two hypotheses concerning the arrangement of the internal nodes of “New Zealand” can now be judged in relation to this area cladogram. Hypothesis 2 is clearly more consistent with Fig. 5b. Under hypothesis 2 the nodal (geological) sequence is east Gondwana–west Gondwana, east Gondwana – Melanesian Rift, and Melanesian Rift–Melanesian Arc. Hypothesis 1 results in both basal and derived east Gondwana–west Gondwana splits a pattern that does not make much sense without invoking several hypotheses of extinction. The weight of available evidence suggests that *P. aucklandicus* has evolved from its ancestor relatively recently (i.e., 20 Ma) following amalgamation and dispersal of *P. obscura* onto the Campbell Plateau.

Biogeography of the *P. angulata* clade

The distributions of the five species in the *P. angulata* clade are restricted to South Island localities west of the Alpine fault (Fig. 3). Geologically this region has undergone cycles of mountain building and erosion and is different from the eastern portion of the South Island. The oldest rocks are Precambrian sediments that were intruded by mid-Palaeozoic granites emplaced during the Tuhua Orogeny (Suggate 1978). Another cycle occurred during the Mesozoic Rangitata Orogeny when the area was part of coastal Gondwana. These mountains became progressively eroded, culminating in peneplanation and the deposition of extensive coal deposits at the end of the Cretaceous (Suggate 1978). It was during this time that the Melanesian Rift became isolated and detached from east Gondwana.

The *P. angulata* clade is distributed in two regions that differ topographically and biologically. *Priasilpha angulata* is the most primitive member of its clade and is restricted to Westland. This locality is of lower altitude than other West Coast localities and shows the effects of extensive glaciation. It does not have beech forest that typifies much of the South Island, but rather the mixed podocarp forests that are present in North Island and extend southward along the west coast of the South Island and at lower altitudes. The West Coast “beech gap” is believed to have formed when all vegetation was extirpated during Pleistocene glaciations (McGlone 1985).

The remaining members of the *P. angulata* clade are distributed mainly in montane forest habitats

(Table 1) composed of fault-bounded, dissected granite batholiths (Suggate 1978). The original ancestor of these taxa may have been similar to *P. angulata*, and were already wingless and had little capacity for dispersal. It is possible that speciation of this group may be relatively recent and was under the control of faulting and translocation associated with the Kaikoura Orogeny within the last 20 Ma (Suggate 1978).

Tying geological history with distribution of all of the members of the *P. angulata* clade is not possible because the structural development of faulting and any horizontal movement in the area is not entirely known. Meanwhile, it remains a mystery as to why the most primitive member of the clade, *P. angulata*, is distributed in an area where the vegetation may have been ablated by glaciers. It is possible that *P. angulata*, along with other members of the biological community in the area, has been isolated for the past 80 Ma (Suggate 1978), is a glacial survivor that thrived in a glacial refugium located west of the present-day coastline.

Body shape

Perhaps the most striking pattern resulting from our analysis is the serial change in body shape from elongate in basal species to ovate in derived species as shown in Fig. 2 and as supported by the regression analysis (Fig. 4). Other measures of body shape could have been made, but, because there are so few specimens of some of the species, performing a full morphometric study is beyond the available museum material. We included some continuous characters that were gap-coded for scoring in the data matrix that could have biased our results by being correlated with body shape. These are characters 9, 10, 14, and 15. To test potential bias due to character correlation these characters were deleted from the data matrix and the analysis was re-run. This deletion experiment resulted in the same tree as that shown in Fig. 2 (tree length = 33, consistency index = 0.57, retention index = 0.56) demonstrating that the morphocline appears is a real phylogenetic trend towards roundness.

Sexual dimorphism in *Priasilpha* is minimal (males have a 554 tarsal formula whereas females have 555) and the variation in body form is species specific and shows a positive trend associated with clade position in the *P. angulata* group. One

obvious correlate with body form change is the loss of hind wings (Roff 1990) which is prevalent among beetles (e.g., Thayer 1992, Scholtz 2000). There are various body forms or sclerite changes associated with wing reduction in beetles, which is coupled with a reduction or loss of flight musculature, and usually includes body compaction and a close fitting of the elytra with the abdomen, as well as size increases (Leibherr 1988). There are often group-specific changes, such that some taxa become more biconvex or hourglass shaped in dorsal view. While changes in body form have not happened in the three species of *Priastichus* (e.g., Fig. 2), the sister taxon of *Priasilpha* from Tasmania, in the *Priasilpha angulata* group, the overall body form change included a transverse broadening of the body and rounding of the humeral calli in the most derived clade (*C. bufonia* + *C. embersoni*), but this is not accompanied with obvious gigantism or dwarfism.

The evolution of an ovate body form, however, is subsequent to the full loss of hind wings in *Priasilpha*. Southwood (1977) and others have argued that wing-loss may be associated with constant, favourable, and isolated environments. Such an explanation may apply to species of the *P. angulata* clade which have evolved in an environment that has been isolated for approximately 80 million years (see below), and may have had a climate somewhat stabilized against extremes by surrounding ocean. However, the landscapes of New Zealand have been changed profoundly in the Tertiary, with Pliocene submergence and cycles of Pleistocene glaciation (Suggate 1978).

In a recent study, Kingsolver and Pfennig (2004) showed that there is a common trend towards phyletic body increases across many taxonomic groups, but selection for decreased development time may oppose selection for change in size. It is possible that for the *P. angulata* group there was selection for shape, or roundness, rather than change in size. Further study is required to correlate changes in *Priasilpha* body form with fecundity (egg and ovariole size and number), physiology (metabolic rates), ability to compete for resources and/or mates, and avoid predation.

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Appendix

Characters used in Phylogenetic Analysis

Characters are derived from the descriptions in Leschen *et al.* (2005) and some of the external characters are shown in Fig. 1. Aedeagal characters (18-22) are coded as unknown (?) for *P. aucklandicus*, a species that is known only from a single female specimen.

1. Dorsal tubercles. 0, present; 1, absent.
2. Length of antennomere 3 (A3) to length of antennomere 4 (A4). 0, A3 = A4; 1, A3 > A4.
3. Lateral pronotal notch. 0, absent; 1 present.
4. Lateral pronotal sulcus. 0, absent; 1 present.
5. Number of anterior pronotal setal clumps or tubercles. 0, two; 1, four.
6. Scutellum. 0, fully exposed; 1, reduced.
7. Hypomeron. 0, not glabrous; 1, glabrous.
8. Prosternal groove. 0, absent; 1, present.
9. Width of mesoventral process (mp) to width of mesocoxa (mc). 0, mp < mc; 1, mp > mc.
10. Relative width of elytra determined by dividing

the elytral length by the elytral width. 0, 1.1-1.8; 1, 0.6-0.9. This character is gap coded and based on the measurements provided by Leschen *et al.* (2005).

11. Elytral bases. 0, parallel; 1, not parallel.
12. Humeral carina. 0, absent; 1, present.
13. Number of elytral tubercles or setose clumps. 0, 7-12; 1, 4-6. This character is gap coded.
14. Width of epipleuron (ep) to the width of the metacoxa (mc). 0, ep < mc; 1, ep > mc.
15. Width of the abdominal process (ap) to the width of the metacoxa (mc). 0, ap < mc; 1, ap > mc.
16. Plane of abdominal ventrites. 0, same; 1, different.
17. Colouration of femora. 0, unicoloured; 1, bicoloured.
18. Anterior keel of penis. 0, absent; 1, present.
19. Anterolateral rim of penis. 0, present to base; 1, present to basal 1/3.
20. Posterior carina of penis. 0, present; 1, absent.
21. Posterior carina of penis. 0, narrow; 1, broad; ?, inapplicable for taxa coded as 20-1.
22. Posterior shape of penis in lateral view. 0, pointed; 1, acute; 2, rounded.