

Taxonomic status of the chafer
beetles *Prodontria modesta* and
P. bicolorata

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ABSTRACT

The status of two particular taxa of *Prodontria*, *P. modesta* Broun and *P. bicolorata* Given, which are found narrowly in the vicinity of Alexandra, has been contentious since *P. bicolorata* was first described. This report reviews the taxonomic status of these two taxa, particularly in the light of recent genetic work, and recommends further research to clarify the situation. Although morphological differences consistent with there being two discrete taxa have been claimed, under many other species concepts the two taxa would be regarded as conspecific. A fuller geographic survey employing the morphological and statistical analyses already used is recommended, including, if possible, sites from further afield, to minimise the possibility of hybridisation and to increase the generality of the conclusions. In concert with the morphological analyses, mitochondrial DNA sequence analysis should be carried out on a small subset of animals from each location. If a clinal pattern of hybridisation emerges, more animals from mixed or contact regions could be examined.

Keywords: chafer beetle, *Prodontria*, *P. bicolorata*, *P. modesta*, species status, morphological analysis, mitochondrial DNA sequence analysis.

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1. Background

Prodontria Broun (Coleoptera: Scarabaeidae: Melolonthinae) is a genus of flightless chafer beetles endemic to New Zealand's South Island (Emerson & Barratt 1997). Two particular taxa, *P. modesta* Broun and *P. bicolorata* Given, are found narrowly in the vicinity of Alexandra. The status of these two taxa has been contentious since *P. bicolorata* was first described (Given & Hoy 1952). At a deeper phylogenetic level, generic limits with respect to *Odontria* (flighted chafers) also need to be re-considered in the light of mtDNA data (Emerson & Wallis 1995).

Being endemic to the Alexandra area, *P. bicolorata* is under threat from horticulture, viticulture, and airport extensions there. Further survey work and recommendation of a reserve area have been identified as important research topics (rank 1+) (Sherley 1989). Survey work was similarly recommended for *P. modesta*.

The purpose of this report is to review the taxonomic status of these two taxa, particularly in the light of recent genetic work, and to recommend further research to clarify the situation. Systematists have suggested at least 22 published species concepts (Mayden 1997). Throughout this review I shall make it clear which particular concept I am referring to by reference to the partial list of concepts in Appendix 1.

2. Morphological evidence

There have been doubts about the taxonomic significance of the morphological differences since *P. bicolorata* was first described (Given & Hoy 1952). In his redescription of *P. modesta*, Given himself says:

‘This species is exceedingly close to *bicolorata*, with which the female in the Lewis Collection appears to be almost identical’ (Given & Hoy 1952, p. 57).

In his description of *P. bicolorata*, he says:

‘Morphologically difficult to distinguish from *modesta* except in the following features:’ (Given & Hoy 1952, p. 58).

Watt (1979) voiced similar feelings:

‘*P. lewisi*, *P. bicolorata* Given, and *P. modesta* (Broun) comprise a group of closely related allopatric species; in fact the two latter may eventually prove to be geographical variants of a single species.’ (Watt 1979, p. 23).

Watt was an experienced coleopterist who had spent much time in the Alexandra area, and his assessment carries some weight (Tony Harris, pers. comm.).

In a systematic paper describing seven new species of *Prodontria*, the two taxa were formally synonymised under the older species name, *P. modesta* (Emerson

& Barratt 1997). This synonymy was based on genetic data and principle component analysis (PCA) of measurement data (Emerson & Wallis 1994).

More recently, C. Jamieson (unpubl. report) has reported fine morphological distinctions in the male genitalia and antennae of the two taxa at different sites near Alexandra. *P. bicolorata* from the Airport site has a shoulder emerging from the neck of the basal shield that is not seen in the Crawford Hills Road site (*P. modesta*). The mixed Conroy's population was variable for this feature. Differences were also observed in the lengths and angles of antennal lamellae. PCA showed differences among the three populations. In particular, the Airport population was smaller, but variance ascribable to differences in leg length, elytra width and head length were found. Jamieson also describes differences in resource response at the two sites. Thus, under morphological or ecological (Van Valen 1976) concepts of species, Jamieson has a case to reverse the synonymy.

One of the more striking differences between *P. modesta* and *P. bicolorata* is in colour: the former is dark whereas the latter tends to be two-toned (dark and light). Systematists defining species on the basis of differences in pelage or plumage colour, particularly in the case of dark varieties, have often been proved wrong in the past (Avisé & Nelson 1989; Laerm et al. 1982). Some New Zealand weta show geographic variation in colour (King et al. 1996; Morgan-Richards & Gibbs 1996); in the case of *Hemideina maori*, this colour difference correlates with a genetic difference in a geographically limited zone of contact, constituting a hybrid zone (King et al. 1996). Some New Zealand Coleoptera show melanism on certain backgrounds (Harris 1988), leading to geographic variation (Harris & Weatherall 1991).

3. Genetic evidence

With instances like the above in mind, and given the contentious taxonomic history of the species, Emerson & Wallis (1994) undertook an isozyme analysis of *P. modesta* and *P. bicolorata* from several locations in the vicinity of Alexandra. They adopted an *F*-statistic approach, which involved partitioning the genetic diversity found at three hierarchical levels: within-population samples, among-population samples within morphs, among morphs (Emerson & Wallis 1994). In short, they found large differences in among-population samples ($F_{ST} = 0.33$), but this was mainly explained by differentiation among population samples within morphs (mean $F_{ST} = 0.265$) rather than differentiation between morphs ($F_{MT} = 0.079$). Most tellingly, they sampled beetles from two locations where both morphs were found (Conroy's Gulley and Hawley Road). In neither of these locations were there significant allele frequency differences between morphs: i.e. the two morphs were sharing gene pools locally, even though there was ample scope for differentiation shown by inter-population differences. So, under the biological species concept (Mayr 1942), which emphasises both the potential for interbreeding among (conspecific) populations and reproductive isolation among species, the two

morphs would be considered conspecific. This interfertility constitutes an intrinsic cohesion mechanism, also symptomatic of conspecifics under the cohesion species concept (Templeton 1989). Under the recognition concept of species (Paterson 1985), which emphasises shared fertilisation systems in species diagnosis, the populations would be considered conspecific. Under the genotypic cluster concept of species, which emphasises bimodality of marker distribution (Mallet 1995), there is no clear gap between the morphs, so they would similarly be diagnosed as conspecific.

4. Phylogenetic evidence

The general acceptance of phylogenetic principles in taxonomy and the development of phylogenetic methodology and molecular techniques has led to various formulations of a phylogenetic species concept, PSC (Cracraft 1983; McKittrick & Zink 1988). The important features of the PSC are monophyly and diagnosability. The mtDNA COII sequence analysis of the genus is instructive in this regard (Emerson & Wallis 1995). This analysis found that *P. modesta* and *P. bicolorata* were sister taxa, and that their sequences differed only by 0.85% (five transition changes), the lowest value in the study. However, this value derives from a comparison of single representatives from each taxon. Resolution of species status under the phylogenetic species concept requires much wider sampling of mitochondrial genomes.

5. Hybridisation scenario

The case for synonymy came largely from the genetic analysis of the Conroy's Gulley and Hawley Road samples (Emerson & Wallis 1994). The F_{ST} analysis and small COII difference are more circumstantial evidence. It is the 'genetic' species concepts that favour synonymy in these circumstances. The apparent absence of consistent morphological differences could be due to insufficient scrutiny by Emerson & Wallis (1994). Another possible interpretation of the Conroy's Gulley and Hawley Road samples, and one favoured by C. Jamieson (pers. comm.), is that they represent a hybrid swarm. This hybridisation could represent a stable ancient hybrid zone (Barton & Hewitt 1985), or the result of more recent habitat modification (Rhymer & Simberloff 1996). In their figure 1 (Emerson & Wallis 1994) in particular, it is possible to read a cline (high *Pep*100 to high *Pep*83) from Flat Top Hill in the south to Strathclyde in the north. This cline encompasses the full range of the two taxa, suggesting widespread introgression. Also, populations to the east are genetically quite distinct again: *Pep*92 and *Pep*77 dominate here. In general terms, *P. modesta* samples to the west of the Clutha are if anything more like *P. bicolorata* than they are like the Crawford Hills *P. modesta* population. So, if hybridisation of two previously

differentiated forms has occurred, the mixing is likely to be widespread, and 'pure' populations of either species may be hard to find.

Hybridisation is a fascinating and useful phenomenon for evolutionary biologists, but it creates problems for systematists and conservation biologists alike: it blurs the neat groupings that both would like and compromises phylogenetic integrity. Literal interpretation of the US Endangered Species Act of 1973 provided loopholes for various land-use agencies to petition for removal of endangered taxa with hybrid ancestry from the list: red wolf and Florida panther were two high-profile species threatened in this way. Pressure was brought to bear to change this 'hybrid policy' (O'Brien & Mayr 1991), which has now been suspended indefinitely (O'Brien et al. 1996).

One feature of hybridisation that should be considered in conservation is its 'naturalness'. Occasional hybridisation among sympatric species, or stable hybrid zones, are common natural phenomena. However, many cases of hybridisation result from recent habitat modification or introduction of related alien species. Introduced mallard are interbreeding with and replacing native grey duck (Hitchmough et al. 1990; Rhymer et al. 1994); black stilt are mixing with pied stilt (Avis 1995; Wallis 1999a); the Chathams endemic Forbes parakeet is threatened by introgressive hybridisation with red-crowned parakeet as a result of forest reduction (Boon et al. 2001; Triggs & Daugherty 1988); yellow-crowned and red-crowned parakeets have almost totally merged on the Auckland Islands (Avis 1995). The introduced common blue butterfly is moving south at the expense of the endemic southern blue (Gibbs 1987).

Recommendation 4 in a DOC discussion paper on management of hybridisation states:

'Where hybridisation is occurring and human impacts have been implicated and either species is threatened, if the technology exists to mitigate the threat the Department should be obliged to do so.' (Avis 1995)

6. Conclusions and recommendations

When Emerson & Wallis (1994) set out to look for genetic differences between these two taxa, they did so on a background of the taxonomy being questioned (B. Patrick, pers. comm.). When their isozyme analysis failed to find consistent differences, and this inability to distinguish the taxa extended to morphology, and very similar COII sequence, they concluded that the systematic status remained questionable, and pointed out that under many species concepts, the two taxa would be regarded as conspecific. Emerson & Barratt (1997) went further and formally synonymised the taxa.

C. Jamieson's recent morphological analysis (unpubl. report) has revealed small differences consistent with there being two discrete taxa. Whereas the type of genitalia difference being described is not used much for this group, antennal

differences can be important (B. Barratt, pers. comm.). However, more detail is needed on consistency among beetles within a site, and the analysis is performed on only a single representative population of each taxon. Fine-scale morphological differences between locations, driven by an interplay of genes, ontogeny and environment, are always possible within species. Systematics as a modern non-typological pursuit concerns the partitioning of diversity, be it morphological or genetic, among populations within taxa and among taxa. Hence, Jamieson needs to show the generality of these morphological differences across several geographic samples. Repeated co-occurrence of taxon-specific sets of traits is an expectation of two taxa.

If in fact two taxa with discrete evolutionary histories have existed in the Alexandra region for some period of time, even if they only diverged in the Pleistocene, we would expect to find two distinct genotypes. The situation here is confused by local differentiation and possible hybridisation, which in itself can produce novel alleles (Woodruff 1989). Hybridisation results in mixing and blurring of the species boundaries, and the evolutionary history is lost. The mitochondrial genome, however, evolves quickly (Brower 1994; Brown et al. 1979), and does not recombine (though see Wallis 1999b). This means that a widespread geographic survey of the two taxa should reveal two discrete clades of mtDNA types, probably matching the two sequences already found (Emerson & Wallis 1995). Although mitochondrial haplotype is completely decoupled from the nuclear genome, and there are many examples of mitochondrial genomes crossing species boundaries (Avice 1994), one would expect to find mainly one type in the region of the Airport at Alexandra, and mainly another type to the east and south.

Finally, in C. Jamieson's unpublished report, there is an allusion to mendelian ratios suggesting a population polymorphism. As Hardy and Weinberg simultaneously showed in 1908, allele frequencies in populations are decoupled from dominance relationships of alleles. That is, for any observed population phenotype frequencies, there are two equally viable inferences of genotype frequencies for either allele being dominant. In any case, it makes absolutely no sense to talk about populations showing a 3:1 mendelian ratio, even if the dominance relationship is known, because the population derives from numerous different mating combinations.

I recommend that a fuller geographic survey employing the morphological and statistical analyses used by Jamieson should be made. I would suggest analysing the same geographic sites as Emerson & Wallis (1994). If possible, it would be useful to include sites from further afield, to minimise the possibility of hybridisation and to increase the generality of the conclusions. With several samples, discriminant functions analyses that attempt to resolve the species clusters can also be employed.

In concert with the morphological analyses, mitochondrial DNA sequence analysis should be carried out on a small subset (2?) of animals from each location. If a clinal pattern of hybridisation emerges, then more animals from mixed or contact regions could be examined.

7. References

- Avise, J.; Nelson, W. 1989: Molecular genetic relationships of the extinct dusky seaside sparrow. *Science* 243: 646-648.
- Avise, J. C. 1994: Molecular Markers, Natural History and Evolution. Chapman & Hall, New York.
- Avis, M. 1995: The Department of Conservation's management of hybridisation. Department of Conservation, Wellington.
- Barton, N.H.; Hewitt, G.M. 1985: Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16: 113-148.
- Boon, W.M.; Kearvell, J.C.; Daugherty, C.H.; Chambers, G.K. 2001: Molecular systematics and conservation of kakariki (*Cyanoramphus* spp.). Department of Conservation, Wellington. 46 p.
- Brower, A.V.Z. 1994: Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Sciences USA* 91: 6491-6495.
- Brown, W.M., George. M. Jr; Wilson, A.C. 1979: Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences USA* 76: 1967-1971.
- Cracraft, J. 1983: Species concepts and speciation analysis. Pp. 159-187 in: R. F. Johnston, R.F. (ed.) Current Ornithology. Plenum, New York.
- Emerson, B.; Barratt, B. 1997. Descriptions of seven new species of the genus *Prodontria* Broun (Coleoptera: Scarabaeidae: Melolonthinae). *The Coleopterists Bulletin* 51: 23-36.
- Emerson, B. C.; Wallis, G.P. 1994: Species status and population genetic structure of the flightless chafer beetles *Prodontria modesta* and *P. bicolorata* (Coleoptera; Scarabaeidae) from South Island, New Zealand. *Molecular Ecology* 3: 339-345.
- Emerson, B. C.; Wallis, G.P. 1995: Phylogenetic relationships of the *Prodontria* (Coleoptera; Scarabaeidae; Subfamily Melolonthinae), derived from sequence variation in the mitochondrial cytochrome oxidase II gene. *Molecular Phylogenetics and Evolution* 4: 433-447.
- Gibbs, G. 1987: Butterfly blues. *Forest and Bird* 18: 18-20.
- Given, B.B.; Hoy, J.M. 1952. A revision of the Melolonthinae of New Zealand. *New Zealand Department of Scientific and Industrial Research Bulletin* 102: 172 p.
- Hardy, G.H. 1908: Mendelian proportions in a mixed population. *Science* 28: 49-50.
- Harris, A.C. 1988: Cryptic colouration and melanism in the sand-burrowing beetle *Chaerodes trachyscelides* (Coleoptera: Tenebrionidae). *Journal of the Royal Society of New Zealand* 18: 333-339.
- Harris, A.C.; Weatherall, I.L. 1991: Geographic variation for colour in the sand-burrowing beetle *Chaerodes trachyscelides* White (Coleoptera: Tenebrionidae) on New Zealand beaches analysed using CIELAB L* values. *Biological Journal of the Linnean Society* 44: 93-104.
- Hitchmough, R.A.; M. Williams, M.; Daugherty, C.H. 1990: A genetic analysis of mallards, grey ducks, and their hybrids in New Zealand. *New Zealand Journal of Zoology* 17: 467-472.
- King, T.M.; Wallis, G.P.; Hamilton, S.A.; Fraser, J.R. 1996: Identification of a hybrid zone between distinctive colour variants of the alpine weta *Hemideina maori* (Orthoptera: Stenopelmatidae) on the Rock and Pillar range, southern New Zealand. *Molecular Ecology* 5: 583-587.
- Laerm, J.; Avise, J.C.; Patton, J.C.; Lansman, R.A. 1982: Genetic determination of the status of an endangered species of pocket gopher in Georgia. *Journal of Wildlife Management* 46: 513-518.

- Mallet, J. 1995: A species definition for the modern synthesis. *Trends in Ecology and Evolution* 10: 294-299.
- Mayden, R.L. 1997: A hierarchy of species concepts: the denouement in the saga of the species problem. Pp. 381-424 in: Claridge, M.F.; Dawah, H.A.; Wilson, M.R. (eds) *Species: The Units of Biodiversity*. Chapman & Hall, London.
- Mayr, E. 1942: *Systematics and the origin of species*. Columbia University Press, New York.
- McKittrick, M.C.; Zink, R.M. 1988. Species concepts in ornithology. *Condor* 90: 1-14.
- Morgan-Richards, M.; Gibbs, G.W. 1996. Colour, allozyme and karyotype variation show little concordance in the New Zealand giant scree weta *Deinacrida connectens* (Orthoptera: Stenopelmatidae). *Hereditas* 125: 265-276.
- O'Brien, S.J.; Martenson, J.S.; Miththapala, S.; Janczewski, D.; Pecon-Slattery, J.; Johnson, W.; Gilbert, D.A.; Roelke, M.; Packer, C.; Bush, M.; Wildt, D.E. 1996: Conservation genetics of the Felidae. Pp. 50-74 in: Avise, J.C.; Hamrick, J.L. (eds) *Conservation Genetics - Case Histories from Nature*. Chapman & Hall, New York.
- O'Brien, S.J.; Mayr, E. 1991: Bureaucratic mischief: recognizing endangered species and subspecies. *Science* 251: 1187-1188.
- Paterson, H.E.H. 1985: The recognition concept of species. Pp. 21-29 in: Vrba, E.S. (ed.) *Species and Speciation*. Transvaal Museum, Pretoria.
- Regan, C.T. 1926: Organic evolution. Pp. 75-86 in: Report on the British Association for the Advancement of Science (1925).
- Rhymer, J.M.; Simberloff, D. 1996: Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* 27: 83-109.
- Rhymer, J.M., Williams, M.J.; Braun, M.J. 1994: Mitochondrial analysis of gene flow between New Zealand mallards (*Anas platyrhynchos*) and grey ducks (*A. superciliosa*). *Auk* 111: 970-978.
- Sherley, G. 1989: Important conservation research topics on terrestrial arthropod species in New Zealand. Department of Conservation, Wellington.
- Templeton, A.R. 1989: The meaning of species and speciation: A genetic perspective. Pp. 3-27 in: Otte, D.; Endler, J.A. (eds) *Speciation and its Consequences*. Sinauer, Sunderland, Mass.
- Triggs, S.J.; Daugherty, C.H. 1988: Preliminary genetic analysis of New Zealand parakeets. Department of Conservation, Wellington.
- Van Valen, L. 1976: Ecological species, multispecies, and oaks. *Taxon* 25: 233-239.
- Wallis, G.P. 1999a. Genetic status of New Zealand black stilt (*Himantopus novaezelandiae*) and impact of hybridisation. Department of Conservation, Wellington.
- Wallis, G.P. 1999b. Do mitochondrial genomes recombine? *Trends in Ecology and Evolution* 14: 209-210.
- Watt, J.C. 1979: Conservation of the Cromwell chafer *Prodontria lewisi* (Coleoptera: Scarabaeidae). *New Zealand Journal of Ecology* 2: 22-29.
- Weinberg, W. 1908: Über den Nachweis der Vererbung beim Menschen. *Jahreshefte Verein Naturkunde Württemberg* 64: 368-382.
- Woodruff, D.S. 1989: Genetic anomalies associated with *Cerion* hybrid zones: the origin and maintenance of new electromorphic variants called hybridzymes. *Biological Journal of the Linnean Society* 36: 281-294.

Appendix 1. Species concepts

Morphological (phenetic, typological)

‘A species is a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name.’ (Regan 1926)

Biological

‘Species are groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups.’ (Mayr 1942)

Ecological

‘A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range.’ (Van Valen 1976)

Phylogenetic

‘A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.’ (Cracraft 1983).

Recognition

‘A species is that most inclusive population of individual biparental organisms which share a common fertilization system.’ (Paterson 1985).

Cohesion

‘A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms.’ (Templeton 1989).

Genotypic cluster

‘Species are groups that remain recognizable in sympatry because of the morphological and genotypic gaps between them.’ (Mallet 1995)