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Number / Nama 39

Molytini

(Insecta: Coleoptera: Curculionidae: Molytinae)

R.C. Craw

Otago Museum P.O. Box 6202, Dunedin, New Zealand



Lincoln, Canterbury, New Zealand

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Cataloguing in publication

CRAW, R.C. (Robin Charles)

Molytini (Insecta: Coleoptera: Curculionidae; Molytinae) / R.C. Craw

- Lincoln, Canterbury, N.Z.: Manaaki Whenua Press, 1999.

(Fauna of New Zealand, ISSN 0111-5383; no. 39).

ISBN 0-478-09325-X

I. Title II. Series

UDC 595,768.23(931)

Prepared for publication by the series editor (and completed by Trevor Crosby) using computer-based text processing, layout, scanning, and printing at Landcare Research, Mt Albert Research Centre, Private Bag 92170, Auckland, New Zealand

Māori text by H. Jacob, Huatan Consultants, Wellington.

Published by Manaaki Whenua Press, Landcare Research, P.O. Box 40, Lincoln, Canterbury, N.Z. Website: http://www.mwpress.co.nz/

Printed by GP Print Ltd, Wellington

Front cover: Lyperobius townsendi (Illustrator: D.W. Helmore).

Publication of the Fauna of New Zealand series is supported by the Foundation for Research, Science and Technology under contract number C09617.

Class Insecta
Order Coleoptera
Family Curculionidae
Subfamily Molytinae
Tribe Molytini

Molytine weevils

These flightless weevils are some of the largest beetles in New Zealand, and they are some of the largest members in the world of their tribe Molytini. Adult speargrass weevils (genus *Lyperobius*) can range in colour from a red-brown to black, and many species have elegant white stripes on their backs, whereas adult karo and knobbled weevils (genus *Hadramphus*) are predominately dark brown with triangular or rounded tubercles on their sides and backs.

This study redescribes the twelve known species and provides descriptions of eight new speargrass weevils. How to identify these weevils is covered in detail, and there is a key to the known and new kinds. Habitus drawings of these weevils, as well as detailed illustrations of key external and internal features, are provided.

As the popular name speargrass weevil implies, adults of most species feed on the rigid spiky leaves and large flowering heads of speargrasses or spaniards (taramea), and they are sometimes also found on kopoti. Grubs of most species feed on roots and the growing leaf crown of these members of the carrot family (Apiaceae), whereas the karo weevil grubs bore in the trunks of karo trees on the Poor Knights Islands.

These weevils are known to occur in insular habitats from the subtropical Poor Knights Islands off the Northland coast, to the isolated Chatham Islands in the east, and the cold subantarctic Snares Islands in the south. They are most numerous and diverse in the South Island mountains, with maximum species diversity in West Otago and Fiordland.

An attempt to reconstruct the genealogy of these weevils is presented. Using this genealogy as a basis, the ecological and biogeographic history of their divergence

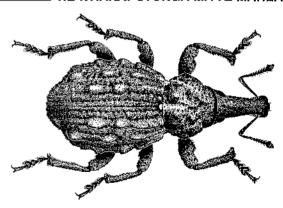


Illustration / Whakaahua: Hadramphus tuberculatus (Illustrator / Kai-whakaahua: Des Helmore).

Ngā 'wīwhara' Molytine

Ko ënei wīwhara rere-kore ētahi o ngā pītara rahi rawa atu o Aotearoa. Huri i te ao, ko rātou anō ētahi o ngā mea tino rahi o tō rātou iwi e kīia nei ko Molytini. Ina tirohia ngā wīwhara noho taramea (o te puninga *Lyperobius*), ko ngā tae o ngā mea pakeke, he kōkōwai, he pango, kei waenga rānei i aua tae e rua. Otirā, arā anō ētahi he ātaahua te tāekaeka haere o te mā me te parauri i ō rātou tuarā. Ko ngā pakeke o te wīwhara noho tahi ki te karo, me te wīwhara pūrekereke (nō te puninga *Hadramphus*), he parauri te tae, otirā, kei te tuarā me ngā kaokao ētahi tona he porohita, he tapatoru rānei te āhua.

I roto i tënei rangahautanga, kua whakaahuatia ä-kupu ngā momo wīwhara Molytine tekau mā rua e mōhiotia ana, tae atu ki ētahi momo hou e waru. Katoa ēnei momo hou, he wīwhara noho taramea. Kua hoatu anō ngā kōrero me ngā whakamārama e mōhiotia ai, e tautuhia ai tēnā me tēnā momo. Arā anō ētahi whakaahua o ēnei wīwhara, me ētahi whakaahua o ngā āhuatanga matua o ō rātou tinana, a waho, a roto anō hoki.

Ko te ingoa kārangaranga tonu o ēnei mea e tohu ana ko te taramea te tino kai a te nuinga o ngā mea pakeke o tēnei momo wīwhara; kainga ai ko ngā rau taratara me ngā pua o te taramea. Heoi anō, ka kitea anō ētahi e noho tahi ana ki te momo tipu e kīia nei ko te kopoti. Ko ngā torongū o te nuinga o ngā wīwhara taramea, ka kai i ngā akaaka me ngā rau hou o ēnei huānga o te whānau kāroti (ko te Apiaceae te ingoa pūtaiao). Engari anō ngā torongū o te wīwhara noho tahi ki te karo — ko tā rātou mahi, he wiri haere, he kaikai haere i ngā kahiwi o ngā karo o Tawhiti Rahi.

(continued overleaf)

(ara haere tonu)

in New Zealand is estimated. It is suggested that they are an old group, of at least 65 million years duration in Aotearoa, descended from a widespread ancestral complex of coastal, insular, lowland, and mountainous sites that have long been conspicuous features of our country.

These weevils are generally considered in New Zealand conservation biology as threatened species that are highly vulnerable to the combined impact of rodent predators and habitat modification. One species appears to have become extinct since European settlement. Insect ecologists who have made detailed studies of the knobbled weevil consider that they are good indicators of whether there are rats on an island.

Contributor **Dr Robin Craw** is Honorary Curator of Entomology at the Otago Museum in Dunedin. His past research has included systematic revisions of tussock butterflies and geometrid moths, as well as many publications on the history, method, and theory of biogeography and phylogenetic systematics. Currently he is working on collecting and describing new species of boulder, copper, and black mountain butterflies, and the conservation status of katipo spiders.

Ko te kaituhi nei, a Tākuta Robin Craw, te Kaitiaki o te Wāhanga Mātai i ngā Aitanga a Pepeke i te Whare Pupuri Taonga o Ōtākou, i Ōtepoti. Ko ētahi o āna rangahautanga o ngā tau ki muri, ko te tirotiro anö me te whakahou i ngā whakarōpūtanga o ngā pūrerehua pātītī taranui me ngā pūrerehua 'geometrid'. Kua whakaputa tuhinga hoki e pā ana ki te hītori, ngā tikanga me ngā mātāpono o te 'koioramatawhenua' me ngā pūnaha whakarōpū e pā ana ki te kunenga mai o ētahi mea. Ko tāna mahi i ēnei rā, he kohi, he whakaahua i ētahi momo pūrerehua hou. Ko ēnei momo hou, nō roto i ngā whānau pūrerehua noho toka, ngā pūrerehua kura, me ngā pūrerehua noho maunga he pāngo te tae. Arā anō tētahi kaupapa e whāia ana e ia, ko te tirotiro i te ongeonge haere o te katipō.

He Kupu Āwhina — Glossary

aitanga a Pepeke — generic term for insects koiora-matawhenua — biogeography kōkōwai — red-brown kunenga — evolution monemone noa — obliterated, rendered extinct mōrearea — exposed to danger ongeonge — becoming rare, endangered pāhekeheke — uncertain, unstable pātīfī taranui — tussock grass pūrekereke — knobbled

Kitea ai ēnci wīwhara Molytine i ētahì kāinga taratahi mai i ngā wai pārūrū o te Tai Tokerau kei reira nei ngā moutere o Tawhiti Rahi, ki Te Wharekauri e noho tārake mai ana i te Rāwhiti, puta atu ki ngā wāhi makariri pērā i Ngā Moutere o Snares i te tonga. Kāore he wāhi i tua atu i ngā maunga o Te Waipounamu mō te huhua o ngā wīwhara, tae atu ki te huhua o ngā momo wīwhara. Ā, ko te wāhi kei reira te tino huhuatanga o ēnei momo pītara, ko te takiwā mai i Ōtākou i te Uru ki Te Taka o te Kārahu a Tamatea.

Kua whai te kaituhi kia whakatakotoria mai te whakapapa o ngā wīwhara nei, ā, ka whakamahia te whakapapa nei hei tūāpapa e whakatauhia ai te huhua haere o ēnei mea i roto i ngā tau. Ka tirohia te āhua o tā rātou noho tahi ki te taiao, ki ētahi atu o ngā aitanga a Tāne, me te hōrapa haere o ngā wīwhara i te mata o te whenua i roto i ngā tau mano tiṇi. E whakapaetia ana nō tuauri whāioio ngā wīwhara nei — arā, kua neke atu i te 65 miriona tau e noho ana i Aotearoa. E whakapaetia ana anō hoki i nohoia e ō rātou tīpuna ngā wāhi maha tonu — ko te tahamoana tēnā, ko ngā moutere me ērā atu wāhi tārake tēnā, ko ngā whenua tāpotupotu tēnā, tae atu ki ngā pae maunga.

I roto i ngā mahi rauhī i ngā aitanga a Tāne i Aotearoa, e whakaaetia ana e te nuinga he pāhekeheke te āhua o te noho mai o ēnei momo pītara ki te ao. E noho mōrearea ana hoki i te ngau mai o ngā āhuatanga kino ki a rātou, pēnei i te kiore, tō rātou tino hoariri, me ngā mahi whakarerekē i te āhua o ō rātou kāinga noho. Arā tētahi momo e whakaarotia ana i monemone noa i muri i te taenga mai o te Pākehā. Tērā ētahi tohunga tirotiro i ngā aitanga a pepeke kua āta rangahau i te wīwhara pūrekereke, ā, e ai ki tā rātou, ka noho tēnei momo wīwhara hei waitohu mehemea e nohoia ana tētahi moutere e te kiore, kāore rānei. (Arā nē, mehemea kei te nui ngā wīwhara pūrekereke, karekau pea he kiore, ā, mehemea korekore ana he wīwhara, kei reira pea te mahi a te kiore.)

tāekaeka — striped
tārake — isolated, remote
Tawhiti Rahi — Poor Knights Islands
Te Taka o te Kārahu a Tamatea — Fiordland
tona — tuberele
tuauri whāioio — very ancient times
whenua tāpotupotu — lowland
wīwhara — weevil

Translation by **H. Jacob** Huatau Consultants, Wellington

ABSTRACT

New Zealand's coxella, karo, knobbled, and speargrass weevils are revised. Sixteen species are recognised in the genus Lyperobius Pascoe, 1876, of which eight are new (australis, barbarae, clarkei, eylesi, glacialis, montanus, patricki, and townsendi). Four species are recognised in the genus Hadramphus Broun, 1911. Karocolens Kuschel, 1987, based on K. pittospori Kuschel, 1987, is reduced to synonymy with Hadramphus, and the new combination H. pittospori is proposed. Lyperobius aciphyllae Broun, 1917 is a subjective synonym of L. cupiendus Broun, 1886. Genera and species are described, and a key to adults is given. Life history, biology, and conservation status and value are reviewed. A numerical phylogenetic analysis exploring the relationships of the two genera and their included species is shown to contain significant phylogenetic structure, against a null hypothesis of random noise, by bootstrapping and tree-length distribution skewness. Biogeographical and ecological history, including host plant shifts, are discussed.

Craw, R.C. 1999. Molytini (Insecta: Coleoptera: Curculionidae: Molytinae). Fauna of New Zealand 39, 68 pp.

CHECKLIST OF TAXA		Methods		
Genus Hadramphus Broun, 1911 Karocolens Kuschel, 1987, new synonymy pittospori (Kuschel, 1987), new combination spinipennis Broun, 1911 stilbocarpae Kuschel, 1971 tuberculatus (Pascoe, 1877) Genus Lyperobius Pascoe, 1876 australis new species barbarae new species carinatus Broun, 1881 clarkei new species coxalis Kuschel, 1987 cupiendus Broun, 1886 aciphyllae Broun, 1917 new synonymy eylesi new species fallax Broun, 1917 glacialis new species hudsoni Broun, 1914 huttoni Pascoe, 1876 montanus new species nesidiotes Kuschel, 1987 patricki new species spedenii Broun, 1917 townsendi new species	21 21 22 22 23 23 24 24 25 26 26 27 27 28 28 29 30 30 31 31	Monophyly of in-group clade Hadramphus + Lyperobius		
		ACKNOWLEDGMENTS		
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Dr K. Morimoto (Kyushu Univerity, Fukuoka, Japan), and Dr C.W. O'Brien (Tallahassee, Florida, U.S.A.). Particular thanks are due to Dr B.I.P. Barratt (BIPB) (AgResearch, Invermay Agricultural Centre, Mosgiel) and Mr B.H. Patrick (BHPC) (formerly of Department of Conservation, Dunedin, now OMNZ) for advice, encouragement, information, and loan of specimens without which this revision would never have been completed. Dr R. Gray (University of Auckland) gave extensive advice and assistance concerning phylogenetic analysis, Correspondence with Dr N. Platnick (American Museum of Natural History, New York) helped clarify nomenclatural implications of the phylogenetic analysis. Mr B.W. Thomas (Landcare Research, Nelson) provided new information on Hadramphus. Referees Dr J.J. Morrone (Universidad Nacional de La Plata, Argentina) and Mr I. Millar (Nelson/Marlborough Conservancy, Department of Conservation, Nelson) made useful comments on the manuscript. Special thanks to Mr D.W. Helmore (Landcare Research, Auckland) for his fine habitus studies and drawings of external morphology.

Abbreviations used above and in citations of specimens examined:

AMNZ Auckland Institute and War Memorial Museum, Auckland, N.Z.

BHPC Brian Patrick private collection, Dunedin, N.Z. Inow in OMNZ!

BIPB Dr Barbara Barratt private collection, Dunedin, N.Z.

BMNH British Museum (Natural History), now The Natural History Museum, London, England

CMNZ Canterbury Museum, Christchurch, New Zealand LUNZ Dept of Entomology, Lincoln University, Lin-

LUNZ Dept of Entomology, Lincoln University, Lincoln, Canterbury, N.Z.

MONZ Museum of New Zealand, Wellington, N.Z.

NZAC New Zealand Arthropod Collection, Landcare Research, Mt Albert Research Centre, Auckland, N.Z.

OMNZ Otago Museum, Dunedin, N.Z.

INTRODUCTION

New Zealand weevils assigned to the tribe Molytini (= Liparini) comprise some of our largest beetles, and some species are among the largest in the tribe. They are conspicuous members of insular, montane, subalpine, and alpine communities. Twenty species in two genera – *Lyperobius* Pascoe, 1876 and *Hadramphus* Broun, 1911 – are recognised in this study, but further undescribed species may occur, particularly in the northern half of the South Island.

Although they are popularly and frequently known as 'giant weevils', this term was originally coincd (in a New Zealand context) as a collective common name for the large subantarctic species of adelognathous (i.e., broadnosed) weevils at present placed in the genera *Heterexis* Broun and *Oclandius* Blanchard (Hudson 1934). Speargrass weevil (for all species of *Lyperobius*), coxella weevil (for *Hadramphus spinipennis*), karo weevil (for *H. pittospori*), and knobbled weevil (for *H. stilbocarpae*) are more accurate common names, and have been used in recent popular treatments (e.g., Meads 1990, Foord 1992).

Previous systematic studies of New Zealand Molytini have been isolated descriptions of genera and species (Pascoe 1876, 1877; Broun 1881, 1886, 1911, 1914, 1917; Kuschel 1971, 1987). Larvae and pupae of some species have been described (May 1971, 1981, 1987a, 1993). Bull (1967) provided a detailed study of the morphology, life history, and biology of *L. huttoni*. The present study is based on examination of more than 1300 adult specimens.

TAXONOMIC DEFINITION OF N.Z. MOLYTINI

Weevils belonging to the tribe Molytini of the curculionid subfamily Molytinaecan be recognised in the New Zealand fauna, and distinguished from offshore Molytini by the following combination of characters.

Adults, Length (excluding rostrum) 11.5-28 mm, greatest width (across elytra) 5.9-12.5 mm, Large, brachypterous, flightless molytine curculionids. Wings rudimentary, narrowly laminate, 0.2-0.65x as long as elytra. Antennae geniculate; funicle with 7 segments, the 7th free from club; club with 3 segments, the 1st longer than remainder of club, the 3rd with a transverse line; sutures straight, oblique. Prothorax with ocular lobes prominent to obsolete. prosternum emarginate. Procoxae contiguous, metacoxae transverse. Tibial apex with uncus and premucro, the uncus arising from a low corbel carina (Fig. 35); distal protibial comb rounded, meso- and metatibial combs obliquely sinuate. Tarsi spongy beneath; 1st segment elongate; 3rd segment much broader than the 2nd, bilobed; 4th segment concealed; 5th segment longer than the 3rd; claws symmetric, free.

Male. Tergite 8 not concealed by tergite 7. Sternite 8 composed of 2 separate sclerotised plates, posteriorly emarginate, with short latero-apical setae. Sternite 9 with asymmetric arms and a sclerotised lobe (Fig. 44, 46). Tegmen complete; parameres well developed, with a short manubrium (Fig. 45, 47). Aedeagus: median lobe weakly sclerotised along dorsal median line (Fig. 58); pedal portion divided laterally by a greatly distensible membrane

(Fig. 64). Endophallus non-eversible, attached to apical margin of aedeagus. Ejaculatory duct inserted dorsally inside proximal arms of heavily sclerotized basal sclerite.

Female. Sternite 8 with 2 sclerotised arms, sometimes fused apically, and bearing short latero-apical setae (Fig. 70–76). Hemisternites long, divided into distinct proximal and distal portions, the distal portion with numerous short setae; short to long membranous hemisternal pouches present. Vagina not extending past hemisternal bases. Bursa copulatrix large, long; spermathecal duct inserted on base of bursa near junction with median oviduct, dilated at insertion point. Spermatheca falciform, much shorter than large spermathecal gland (Fig. 77–83).

Larvae (see, e.g., May 1993, fig. 830–839). Length 17.5–32 mm, width 6.5–10 mm. Body large, robust, dense creamy white; head dark red-brown to black, partially retracted. Frontal suture narrow, not angulate before apex. Dorsoepicranial setae 3 not in contact with frontal suture. Frontal setae 5 well developed. Thoracic segments with a V-shaped pocket medially between the 2 ventral folds. Abdominal segment VIII without prodorsal setae. Spiracles conspicuous, elongate-ovate or subcircular; airtubes conspicuous, with fine, pigmented annuli, directed dorsad (thoracic) or caudad (abdominal); AbdVIII spiracle on dorsum, as large as thoracic spiracle.

Pupae. Maximum length 17–20 mm. Cuticle glabrous; setae dark, tapering, mounted on small tubercles, strongest on head and pronotum, finer on abdomen. Elbows with subequal setae. Pseudocerci on abdominal segment IX short, dark, curved, without associated setae. Antennal club smooth. Primary protheca bullate (*Hadramphus*) or striate (*Lyperobius*), with spinules on dorsal margin and ridges; secondary pterotheca shorter than the primary. [Descriptions of larvae and pupae from May 1971, 1981, 1987a, 1993.]

Host plants. Apiaceae (Aciphylla and Anisotome), Araliaceae (Stilbocarpa), and Pittosporaceae.

Remarks. Pascoe (1876, 1877) placed *Lyperobius huttoni* and *L. tuberculatus* in Lacordaire's (1863) group Molytides, based on Schoenherr's (1823) family-group name for this taxon. The family-group name Liparides (Latreille 1828) – used by Marshall (1932), Solari (1941), Morimoto (1962), and others to refer to a tribe (Liparini) of the subfamily Hylobiniae – is equivalent. An ecophyletic cline from fully flying Hylobinii to flightless Liparini was noted by Morimoto (1982), who associated these two tribes under the family-group name Hylobinii Kirby, 1837; the tribal name Molytini has priority, however. Following

Hudson (1934) and Kuschel (1987) this tribe, as represented in New Zealand, is placed in the subfamily Molytinae.

Larvae of *Hadramphus* and *Lyperobius* can be separated from the superficially similar large larvae of *Anagotus* species (Aterpinae) by (a) having dorsoepicranial setae 3 situated on the epicranium and not within the frontal suture or on the frons, and (b) abdominal segment IX having two dorsal setae, one slightly longer than the other. They are unlikely to be confused, though, because of hostplant differences — no *Anagotus* larvae are found on Apiaceae, Araliaceae, or Pittosporaceae.

Hadramphus and Lyperobius larvae differ from those of the xylophagous Holarctic Hylobius Germar and Nearctic Pachylobius Le Comte mainly in the shape and alignment of the spiracles. They share with Hylobius and its allies conspicuously large airtubes that are often pigmented. Larvae of the European molytine Liparus germanus Linnaeus are very similar also to those of the New Zealand Molytini, having clongate-ovate spiracles in common with Hadramphus larvae (cf. Scherf 1964 and May 1971, 1981, 1987a, 1993).

MORPHOLOGICAL CHARACTERS

Morphological terms useful in taxonomy and identification are illustrated for external features (Fig. 11–13), male genitalia (Fig. 62), and female genitalia (Fig. 78).

A character-based phylogenetic species concept (Baum & Donoghue 1995) is adopted in the context of this study. It defines a species as the smallest aggregation of populations diagnosable by a unique combination of character states in comparable individuals.

Head. The globose head is produced into a rostrum that bears the mouthparts, comprising a triangular pair of bidentate mandibles with tufted or scattered setae on their outer face, paired maxillae each with a three-segmented maxillary palp, and a rectangular mentum bearing a pair of three-segmented labial palps. There is variation between the species in the relative length, thickness, and shape of the rostrum. It can vary from relatively short and thick with an expanded apex (Fig. 14, 15) to relatively long and thin with the apical portion not much more expanded than the base (Fig. 16, 17). A dorsal median carina occurs in some taxa. The geniculate antennae, inserted laterally on the apical third of the cylindrical rostrum, are eleven segmented with the terminal three segments forming a compact club. The first segment, the scape, contributes almost half the antennal length and is inserted at the anterior end of the scrobe, a deep lateral sulcus extending obliquely from the anterolateral portion of the rostrum to the ventral portion of the eye. Segments 2–8 constitute the funicle, and range in shape from elongate to rounded to transverse. The ratio of the length of the first to the second segment, and the shape of the 7th funicle segment can be diagnostic of some taxa. Eyes are lateral, convex, and transverse.

Pronotum. Diagnostic features of the pronotum include differences in the degree of subapical and basal constriction, macro- and microsculpture, and extent of scaling patterns and punctuation. In Lyperobius the pronotum varies from nearly transverse with broadly rounded sides to elongate with narrowly rounded sides; such distinctions are characteristic of particular species and species-groups. Pronotal sculpture and scale patterning vary from three narrow, longitudinal scale-filled sulci (two marginal, one median) (Fig. 21, 24) through the pale scales being confined to broader, shallower impressions (Fig. 19, 20) to being scattered in no particular pattern (Fig. 22, 23). In the four Hadramphus species the propotal sides and disc are ornamented with tubercles which in size, shape, and position are specific to species or species-groups. The ventroanterior lateral margins of the prothorax bear conspicuous ocular lobes which partly conceal the eyes in Hadramphus: these are reduced in Lyperobius.

Elytra. Elytral shape, scale patterns, and modifications of the elytral intervals are all important taxonomic characters. The degree of prominence of elytral humeri, and the development and shape of discal and declivity tubercles, differ greatly between the *Hadramphus* species (Fig. 1–4). The extent and development of raised costae on the even and uneven intervals offer a number of useful distinguishing features in *Lyperobius* (Fig. 5–10, 27, 28). The shape of the pale scales can vary considerably on a single individual, but scale shape is usually relatively constant on the elytral disc, and can serve as a useful diagnostic character.

Legs. The legs can vary from elongate and slender with the femora barely claviform and the tibiae straight (e.g., *H. spinipennis*) to short and thick with the femora gradually claviform (e.g., *L. cupiendus*) and the tibiae short and sinuate (e.g., *L. fallax*). The extent and position of scaling on the upper inner face of the coxae is an important character diagnostic of the *L. coxalis* species-group (Fig. 32–34). Size and shape of the second and third tarsal segments, and the degree of development of the tarsal sole hairs, offer useful diagnostic characters for distinguishing both sympatric congeners and vicarious sister taxa (Fig. 36, 37).

Sexual dimorphism. Apart from minor differences in shape of the rostrum between the sexes, dimorphism is most readily observed in the fifth ventrite. The male ventrites are smaller and much more transverse (Fig. 38, 40, 42) than the female ventrites, which are larger, longer, and more rounded on their margins (Fig. 39, 41, 43).

Genitalia. The male median lobe is stout and robust, as is characteristic of molytine weevils. Size and shape of the median lobe and the development of the aedeagal apodemes relative to the median lobe can be characteristic of a particular species. The shape of the endophallic basal sclerite, and the presence or absence of sclerites in the endophallus apex, can be useful diagnostic characters (Fig. 48–69). In the female genitalia size and shape of the 8th sternite are useful features for distinguishing species (Fig. 70–76). Degree of development of the hemisternal pouches, size and shape of the hemisternites and styli, and the nature of their setation can vary greatly between species (Fig. 77–83).

LIFE HISTORY AND BIOLOGY

Larvae of Lyperobius and of two Hadramphus species (H. spinipennis, H. tuberculatus) feed on herbaceous perennial Apiaceae in the predominantly New Zealand genera Aciphylla and Anisotome. Fouveaux Strait to Snares populations of the southern species H. stilbocarpae are found on the fleshy herb Stilbocarpa (Araliaceae), but southwest Fiordland populations use Anisotome lyallii as a host.

Larvae are found both in the thick main roots and rhizomes of the host plants (Bull 1967, May 1971, 1981) and in soil surrounding the roots (Bull 1967). Larvae of *L. hudsoni* and *L. montanus* have also been found grazing on leaf bases and crowns. *L. huttoni* larvae construct a bare pupal chamber in the soil adjacent to the roots of the host plant. The pupal stage lasts about 2 weeks. After eclosion the teneral adults remain in the chamber for almost 8 months before emerging. The lifespan of adult *L. huttoni* in the wild has been estimated at 2.5 years (Bull 1967).

Larvae of *H. pittospori* are subcortical borers in the live branches, trunks and root crowns of the woody host plant karo (*Pittosporum crassifolium*). Their egg-shaped pupal chambers are found in the centre of the workings. The pupal stage lasts about 3 weeks. Adults of this species have remained alive in captivity for 3 years (Bennett 1987).

Hadramphus adults are nocturnal, whereas those of Lyperobius are diurnal, feeding actively on leaf tissue, flower stems, and developing seeds (Barratt 1985, Bennett 1987, Bull 1967, Meads 1990). Adult L. huttoni employ

two types of feeding - leaf nicking on the outer leaflets of the host, and a deep ovoid notching of the leaf petioles (Bull 1967). Kuschel (1971: 242) described feeding behaviour of H. stilbocarpae as "adults notch leaf margins at night." D.S. Horning (in litt.), who observed this species in the field, notes: "We saw many weevils feeding on Stilbocarna and not one of them was notching the leaf margin. Rather, they fed on the leaf by chewing a hole through it and then enlarging the hole. Often this is close to the leaf margin and the narrow strip between the edge of the feeding hole and the leaf margin may break, creating an illusion that the leaf margin has been notched." Meads' (1990: 49) photograph of this species feeding confirms Horning's account. Adults of this species can congregate in large numbers on a single host plant and feed until it dies (Close 1997).

PHYLOGENETIC ANALYSIS

Methods. An attempt is made to reconstruct the phylogenetic history of Hadramphus and Lyperobius using the methods of Hennig (1966), which group taxa into monophyletic lineages (clades) on the basis of their possession of shared derived character states (synapomorphies). Character state polarities were determined by outgroup analysis as discussed by Watrous & Wheeler (1981), Maddison et al. (1984), and Bryant (1991). When two or more states of a character occur within an ingroup, the state occurring in related outgroups is considered to be ancestral (e.g., characters 12, 13, and 14 in the following list). Equivocal polarity decisions can occur when out-group relationships are poorly resolved and uncertain, such as in this study, and two or more states of a character occur both within and without the ingroup (e.g., characters 5, 7, and 8 in the following list). In these instances the predominantstates method has been applied, i.e., the state occurring most commonly amongst the outgroup taxa is taken to be ancestral for the ingroup (Kluge & Farris 1969).

A representative selection of phenetically related taxa belonging to the tribe Molytini, and related genera from the Pacific Rim and Northern Hemisphere, were selected as outgroups; they are listed in Appendix 1. All these taxa were examined for external characters. Genital characters were studied in detail for four taxa – Liparus, Plethes, Aclees, and Hesychobius. These taxa were selected because they have either a close phenetic resemblance to Lyperobius (Liparus and Plethes) or they are some of the closest relatives in a geographical sense (Aclees and Hesychobius are both found in the southwest Pacific region) to New Zealand taxa. There is also a host and habitat resemblance between Liparus (see Magnano 1954 for details of

distribution) and the New Zealand Molytini, both groups being predominantly insular or montane to subalpine, with many species feeding on plants belonging to or associated with the family Apiaceae.

Monophyly of in-group clade *Hadramphus + Lyperobius*. *Hadramphus* and *Lyperobius* are inferred to be a monophyletic clade on the basis of the following combination of character states.

- (1) Spermatheca falciform, with no marked division into nodulus and ramus. Outgroup taxa have a much more elongate spermatheca with distinctive nodulus and ramus.
- (2) Hemisternites divided into distinct distal and proximal plates (*Lyperobius*, Fig. 77–78; *Hadramphus*, Kuschel 1971, 1987). This condition is not found in any out-group taxa examined, although a somewhat similar state has been noted in the very distantly related Cholinac of the genus *Homalinotus* (Vauric 1973, fig. 92, 94) and Brachyderinae of genus *Cneorhinus* (Alonso-Zarazaga 1988, fig. 1).
- (3) Apical margin of male 8th sternite deeply emarginate medially (*Hadramphus*, Fig. 44, 46; *Lyperobius*, Kuschel 1987). The predominant state in the outgroup taxa and other curculionid subfamilies is for the apical margin to be either rounded or acute.
- (4) Endophallus of male genitalia non-eversible, attached to apical margin of median lobe and contained entirely inside median lobe. According to Kuschel (1987) this condition has not been noted before in curculionids.

Character list and discussion of character state polarity [0 = ancestral; 1, 2, & 3 = derived]

1. Rostrum median carina absent (0) Rostrum median carina present (1)

Hadramphus spinipennis and H. stilbocarpae have a low, median rostral carina. No such carina is found in most outgroup taxa examined. A distinct median carina occurs in the distantly related Rhineilipus cuvieri Boheman and Plinthus meyeleri, and traces of this structure occur in some species of Heilipus (e.g., H. lactarius Germar).

Postocular lobes obsolete (0)
 Postocular lobes well developed (1)

All Hadramphus species have well developed postocular lobes partly covering the eyes. Postocular lobes are absent to obsolete in phenetic and phylogenetic relatives (e.g., Lyperobius, Plethes, Liparus, Anisorrhynchus, Aclees, Hesychobius) but variably present in other molytine gen-

 Pronoturn lateral margins without tubercles but with a constriction at apical third (0)
 Pronoturn lateral margins tuberculate at apical third (1)

era (e.g., Dyscerus, Apterylobius, Heilipodus).

Pronotum lateral margins tuberculate at middle, and widest at middle to apical third (2)

In Lyperobius and many other Molytini the pronotum is slightly constricted laterally at the apical third to quarter. Hadramphus pittospori has a large, acutely angled tubercle in this position and a small, obtusely angled tubercle at the middle (Fig. 1). The other three Hadramphus species possess a large lateral tubercle at the middle of the pronotal margins (Fig. 2–4). The Chilean Calvertius tuberosus (Fairmaire & Germain) has a large, protuberant swelling midway on the pronotal lateral margins, but this does not appear to be homologous with the tubercles found in Hadramphus.

4. Pronotal disc punctate (0)
Pronotal disc with knobs/tubercles (1)

The pronotal disc varies from sparsely to densely to wrinkled punctate in most molytine taxa. Some South American genera (e.g., Byzes, Parabyzes) and Asian species (e.g., Dyscerus perforatus) have their pronotal disc ornamented with large glossy granules that in some taxa (e.g., Helipodus onychinus) are coalesced into raised areas. Only the four Hadramphus species possess four distinct discal knobs/tubercles (Fig. 1-4).

 Metasternal margin in front of hind coxae with a metasternal fold, and sometimes a slight overhang at most (0)

Metasternal margin in front of hind coxae with a distinct projecting tooth (1)

All four *Hadramphus* species possess a projecting tooth on the hind margin of the metasternum directly in front of the hind coxae (Fig. 29). *Lyperobius* and most other molytine taxa have at most a well developed metasternal fold with a slight overhang (Fig. 30, 31). Elsewhere in the Molytini and related groups a projecting metasternal tooth has been noted only in some species of *Orthorhinus* (e.g., *O. aethiops*) and *Byzes* (e.g., *B. diversus*).

Mesepisternum with no distinct impression, at most a few confluent punctures (0)

Mesepisternum with a distinct elongate impression (1) The mesepisternum in *Hadramphus* bears a distinct elongate impression which is often filled with pale scales. This impression has not been observed in other Molytini, which at most have a few confluent punctures forming a very small impression.

7. Elytral scales scattered (0)

Elytral scales confined to even intervals and forming pale scale stripes (1)

Pale scale stripes on at least some of the elytral intervals are found in a variety of weevil taxa belonging to several curculionid subfamilies, e.g., the South African *Eremnus*

lineatus (Eremninae), the New Zealand Anagotus hamiltoni (Aterpinae), and the South American Astyage lineigera (Cholinae). Amongst the immediate outgroup taxa only Plethes albotineata has scale stripes resembling those of Lyperobius. In L. huttoni and L. montanus scale stripes are virtually absent on the elytral disc, occurring only on the clytral declivity in a very reduced state in fresh specimens.

8. Elytral disc intervals (3,5,7) flat to convex (0)
Elytral disc intervals (3,5,7) tuberculate (1)
Elytral disc intervals (3,5,7) costate, with no development of secondary costae in even intervals (2)
Elytral disc intervals (3,5,7) costate, with a tendency

for secondary costae to occur in even intervals (3) Tubercules on the elytral disc do not occur often in the Molytini and related tribes (exceptions: South American genera Byzes, Epistrophus, Placeilipus, Rhineilipus, and Syphorbus, and Plagiophelus from Asia). Such tubercles. formed by irregular elevations of the elytral intervals, are found in all Hadramphus species (Fig. 1-4). Development of elytral intervals as raised costae is not a common character, occurring only sporadically in a variety of curculionid subfamilies, e.g. Astyage lineigera (Cholinae). Lixus lineatus (Cleoninae), several Anagotus species (Aterpinae), and several Sargon species (Brachyderinae). Amongst the immediate outgroup taxa costate clytral intervals are found in Plethes albolineata and P. unguiculatus. Only the uneven elytral intervals are raised as costae in Lyperobius glacialis, L. carinatus, L. fallax, L. eylesi, and the L. hudsoni species-group (e.g., Fig. 6, 8, 10, 27). There is a tendency for the even elytral intervals to be raised as secondary costae - though not all individuals in a population manifest this character state - in the L, spedenii species-group and in L. australis, L. clarkei, and L. nesidiotes (Fig. 5, 9).

- 9. Mid elytral declivity with interval 3 flat to costate (0) Mid elytral declivity with a tubercle on interval 3 (1) Both *Hadramphus spinipennis* and *H. stilbocarpae* have a distinctive conical tubercle about midway on interval 3 of the elytral declivity. This tubercle has not been observed in other Molytini.
- Elytral declivity lateral margin without a tubercle on interval 9 just above articulation of abdominal ventrites 4 and 5 (0)

Elytral declivity lateral margin with a tubercle on interval 9 just above articulation of abdominal ventrites 4 and 5 (1)

Hadramphus pittospori, H. spinipennis, and H. stilbocarpae have a distinctive tubercle on elytral interval 9 just above the articulation of abdominal ventrites 4 and 5. This tubcrele does not occur in *H. tuberculatus*, *Lyperobius*, and other Molytini.

11. Tarsal segments 1 and 2 with apical sole hairs same length as those on segment 3, usually not distally projected (0)

Tarsal segments 1 and 2 with apical sole hairs longer than those on segment 3, projected distally (1)

All members of the *L. hudsoni* species-group have the apical tarsal sole hairs on segments 1 and 2 longer than those on segment 3, and they are projected distally (Fig. 37). This character state is unique to these taxa as compared to other *Lyperobius* species (Fig. 36), *Hadramphus*, *Plethes*, and *Linarus*.

12. Femoral tooth or denticle present (0)

Femoral tooth or denticle absent, represented at most by a low carina (1)

A tooth or denticle is present on the femora of most species of Molytini. In the New Zealand taxa it is found only in *H. pittospori* and *H. spinipennis*.

 Coxae with upper inner face bearing scattered hairs and scales (0)

Coxae with upper inner face bearing a dense scale patch (1)

The three members of the *L. coxalis* species-group share the synapomorphy of a dense, slightly raised scale patch on the upper inner face of all coxae (Fig. 33). This character state has not been observed in any other Molytini (e.g., Fig. 32, 34).

Male 5th ventrite not medio-apically emarginate (0)
 Male 5th ventrite medio-apically emarginate (1)

There is a distinct shallow apical median emargination on the male 5th ventrite of *H. stilbocarpae* and *H. spinipennis* (Fig. 38). This character state has not been observed in the other *Hadramphus* species, *Lyperobius* (Fig. 40, 42), *Plethes, Liparus, Aclees,* and *Hesychobius*.

15. Female 5th ventrite without an upturned, rimmed outer medio-apical margin (0)

Female 5th ventrite with an upturned, rimmed outer medio-apical margin (1)

The medio-apical margin of the female 5th ventrite has an upturned rim (Fig. 43) in members of the *L. coxalis* and *L. spedenii* species-groups and in *L. eylesi*. This character state has not been observed in other *Lyperobius* species (e.g., Fig. 41), *Hadramphus* (e.g., Fig. 39), and other Molytini.

16. Male median lobe endophallus floor at apex beyond ostium without distinct sclerotisations (0)
Male median lobe endophallus floor at apex beyond ostium with distinct sclerotisations (1)

In most genera of Molytini the apical portion of the endophallus beyond the ostium is completely membranous, without any distinct sclerotisations. In *Hadramphus* (Fig. 48–51) and all *Lyperobius* species except for those of the *L. coxalis* and *L. spedenii* species-groups (Fig. 55, 56, 66–68) very distinct sclerotisations are located in the apical portion of the endophallus.

17. Female styli apical (0)

Female styli latero-apical (1)

In *L. carinatus* (Fig. 78) and *L. clarkei* the styli are inserted latero-apically on the gonocoxites. In other *Lyperobius* species (Fig. 77, 79–83), *Hadramphus* (Kuschel 1971, 1987), *Liparus*, *Hylobius*, and *Pissodes* the styli are inserted apically.

Female gonocoxites without pouches (0)
 Female gonocoxites with short pouches (1)
 Female gonocoxites with long pouches (2)

Distinct membranous pouches are located on the proximal portion of the female gonocoxites of all *Hadramphus* and *Lyperobius* species. Two character states, short (e.g., Fig. 77, 79–83) and long (Fig. 78; Kuschel 1971,1987), are recognised. These pouches have not been observed in other Molytini.

19. Female bursa copulatrix without lobes near junction of oviduct (0)

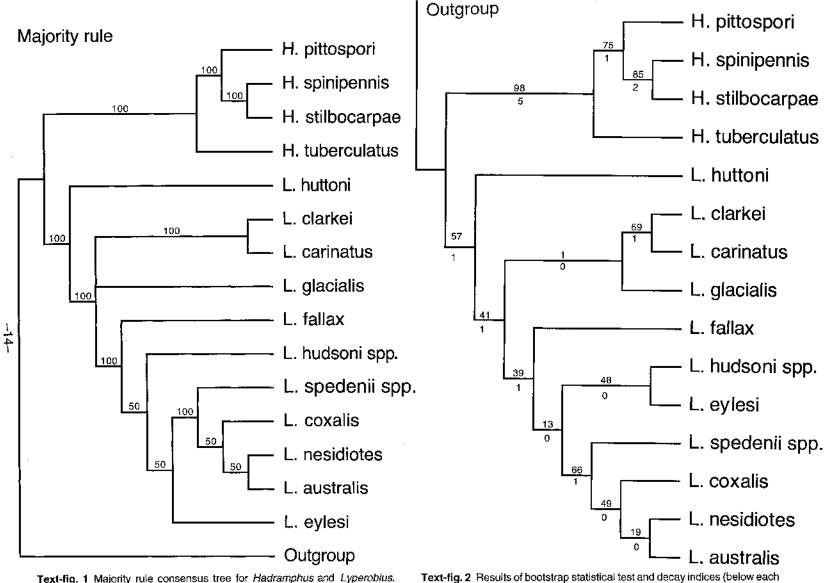
Female bursa copulatrix with lobes near junction of oviduct (1)

Members of the *L. spedenii* species-group are characterised by a lateral pair of lobes on the bursa copulatrix near the junction with the median oviduct (Fig. 79, 81, 82). This character state has not been observed in other *Lyperobius* species, *Hadramphus*, *Liparus*, *Hylobius*, and *Pissodes*.

20. Female bursa copulatrix completely membranous (0) Female bursa copulatrix with distinctive sclerotised area near junction with oviduct (1)

All members of the *L. hudsoni* species-group and *L. eylesi* possess a distinctive female genital character – a distinct internal sclerite at the junction of the bursa copulatrix and the median oviduct (Fig. 77, 80, 83). This sclerite is not found in other *Lyperobius* species, *Hadramphus*, *Liparus*, and *Hylobius*. An internal female genital sclerite in the same position has been observed in *Pissodes piceae*, but it is of a different form to that found in the *L. hudsoni* species-group and *L. eylesi*.

Phylogenetic results and relationships. A data matrix was constructed for 15 *Hadramphus* and *Lyperobius* taxa and an hypothetical outgroup taxon based on 73 species of Molytini and related genera, embodying 20 characters



Text-fig. 1 Majority rule consensus tree for *Hadramphus* and *Lyperobius*. Numbers along branches indicate the percentage of the 16 most parsimonious trees in which each branch occurred.

Text-fig. 2 Results of bootstrap statistical test and decay indices (below each branch) mapped onto majority rule consensus tree. The percentage of 2000 bootstrap samples in which each monophyletic group was represented is shown above each branch.

Trees are unrooted Starting seed = 1 Time used = 3.88 sec

Frequency distribution of lengths of 2000 random trees:

```
# (6)
# (5)
# (6)
50
51
52
53
54
 ## (10)
|#### (15)
55
56
 ### (13)
 ###### (29)
58
59
 ########## (45)
 ############### (46)
 ############# (64)
61
 ############## (72)
 ##################### (85)
64
 ####################### (94)
65
 ############### (79)
 66
 71
 #### (17)
```

mean=66.722000 sd=4.368148 g1=-1.168185 g2=1.069621 using the program AutoDecay 3.03 (Eriksson, n.d.).

Analysis of this matrix produced 16 most parsimonious trees, with a length of 31 steps. A majority rule consensus tree is presented as a summary of phylogenetic relationships (Text-fig. 1). Both genera form monophyletic clades, and species relationships are unequivocal in *Hadramphus*. A decay index of 5 for this clade (Text-fig. 2) indicates that the internal node uniting all *Hadramphus* species into one clade has greatest support, since a tree of length 37 is the shortest without this branch. More problematic are the interrelationships of *Lyperobius* species, but there is only one unresolved trichotomy in the consensus tree.

Statistical tests of phylogenetic structure. A bootstrap test can be used to put confidence intervals on any estimate of phylogeny by resampling the original data set to infer the variability of the estimate. Characters in a matrix of taxa × characters can be sampled with replacement (i.e., bootstrapped) to create many new matrices of the same size as the original. Each of these can then be analysed to find the best fitting tree. Results can then be combined in a majority rule consensus tree. Next to each branch of that tree is shown the number of times that the monophyletic group defined by that branch occurred (Felsenstein 1985). Bootstrap proportions≥70% usually correspond to a probability of ≥95% that the corresponding clade is real (Hillis & Bull 1993).

Judging by published studies, it is frequent for putative monophyletic groups to be found to be supported with less than 95% confidence. This is because utility of this test is limited in data sets lacking large numbers of characters relative to the number of taxa (Sanderson 1989). It has been estimated that even in a data set with no character conflict (i.e., homoplasy), every clade must be supported

Text-fig. 3 Frequency distribution of lengths of 2000 unrooted random trees.

Table 1 Character state distribution matrix for numerical phylogenetic analysis of *Hadramphus* and *Lyperobius*.

000000000000000000000000000000000000000
0444440404000000000000
01111101010000010200
11211101110001010200
1121110111010101010200
01211101000100010100
00000013000110170100
00000012000100011200
00000013000100011200
00000012000110100100
00000012000100110101
00000012000100010100
00000012000100010200
00000012001100010101
00000010000100010200
00000013000110100100
00000013000100100110

(Table 1). Apart from the outgroup taxon, two other consolidated taxa were used for character state scoring. These were *L. hudsoni* spp. (comprising *L. barbarae*, *L. hudsoni*, *L. montanus*, and *L. townsendi*) and *L. spedenii* spp. (*L. cupiendus*, *L. patricki*, and *L. spedenii*). This matrix was analysed in the numerical phylogenetics package PAUP ver. 3.1.1 (Swofford 1993) using the branch and bound algorithm, which guarantees finding all the most parsimonious trees. Decay indices, which indicate the length of the shortest tree lacking a particular node, were calculated

by at least three derived characters for statistical significance at the 95% level to result. Thus, even under ideal circumstances, where character conflict is low or non-existent, phylogenetic analyses with only a moderate number of characters per taxon will exhibit low confidence levels in at least some parts of the resulting tree hypothesis (Penny & O'Kelly 1991).

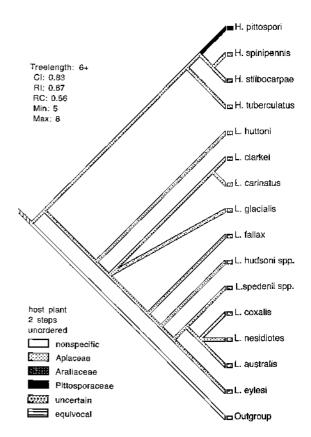
Application of this test to the reported data (Text-fig. 2) reveals that *Hadramphus* species form an extremely well supported clade (98%). The most strongly supported clade within this group is the sister-group relationship *H. spinipennis-H. stillbocarpae* (85%). Support for a *Lyperobius* clade is more equivocal (57%), but within this genus a clade comprising the *L. spedenii* and *L. coxalis* speciesgroups is better supported (66%).

An alternative test, tree-length distribution skewness, can discriminate between character data sets containing phylogenetic signal and those with significant amounts of random noise. Data matrices consistent with one phylogenetic hypothesis produce tree-length distributions that are highly skewed to the left, while those compatible with many phylogenetic hypotheses produce more symmetrical tree-length distributions that cannot be distinguished from those produced by random character data. Skewness of a tree-length distribution can be measured by the g 1 statistic, which is one measure of the skewness of a frequency distribution. Tree-length distribution frequencies that are significantly skewed at the >99% level (g 1 < -0.47) provide a critical value for distinguishing data sets containing phylogenetic structure from those with random noise (Huelsenbeck 1991).

Applying this test to the reported data set resulted in a tree-length frequency distribution with a mean tree length of 66.7 steps, and highly skewed to the left (Text-fig. 3). The g 1 statistic value for this simulation is -1.168, well below the significant critical values reported for this method (Hillis & Huelsenbeck 1992). This value indicates strong support for there being phylogenetic signal in the *Hadramphus-Lyperobius* data set.

HISTORICAL ECOLOGY AND BIOGEOGRAPHY

Methods. Biogeographical, ecological, and evolutionary history in a phytophagous weevil clade can be estimated using a phylogenetic tree derived from morphological or other evidence. This reconstruction of phylogeny gives a critical basis for postulating scenarios of host-plant usage, selection, and shifts (Anderson 1993), as well as other aspects of biogeographic and ecological history (Brown 1995, Morrone & Crisci 1995). Host plants and eleva-



Text-fig. 4 Distribution of host-plant families mapped onto the majority rule consensus tree for *Hadramphus* and *Lyperobius*.

tional ranges (expressed as broad habitat groupings, e.g., lowland, subalpine) are mapped onto the independently derived phylogenetic tree using MacClade (Maddison & Maddison 1992), and ancestral patterns are predicted by specifying states for the interior nodes of the tree. This is equivalent to character state optimisation.

Plant-host analysis. All *Lyperobius* species utilise only members of the Apiaceae as hosts. The most parsimonious interpretation for the postulated history of host shifts in the *Hadramphus* clade involve a shift onto *Pittosporum* (Pittosporaceae) for *H. pittospori*, and onto *Stilbocarpa* (Araliaceae) for *H. stilbocarpae* from ancestral apiaceous host plants (Text-fig. 4).

Speciation and the evolution of host-plant shifts in extant species of *Hadramphus* and *Lyperobius* happened well after the divergence of the higher taxa of the plants on which they feed. These host-plant shifts have occurred among plants that appear very similar in anatomical,

chemical, and embryological features (Harbourne & Turner 1984, Hegnauer 1969, Metcalfe & Chalk 1950). In an analysis of DNA sequences Apiaceae was the closest relative of Araliaceae, and this clade was the sister taxon to Pittosporaceae (Chase et al. 1993). Host-plant relations of New Zealand Molytini offer some support for the hypothesis that chemical similarity and phylogenetic affinity of insects' host plants facilitate host shifts.

Plant hosts for most non-New Zealand Molytini are a wide variety of gymnosperm and herbaceous or woody angiosperm taxa (Anderson 1993). They include Coniferae for the northern temperate genera Hylobius. Hylobitelus, Pissodes, and Pachylobius, Araucariaceae for the Chilean Calvertius, Ficus (Moraceae) for the Asia-Pacific Aclees, and genera of Aceraceae, Oleaceae, Rosaceae, Illiciaceae, and Lauraceae for the Asian Dyscerus (Morimoto 1982). Some plant hosts for genera that are close phenetically to Hadramphus and Lyperobius include Asteraceae and Apiaceae for the Palearctic Liparus (Smreczynski 1968), and the South American Helipodus (rearing label data in NZAC), and Asteraceae for the northern Andean Plethes (rearing label data in NZAC). This crude 'outgroup' comparison provides additional support for the hypothesis, derived from phylogenetic analysis, that the ancestral host plant for the Hadramphus-Lyperobius clade was a member of the Apiaceae.

A review of specialised associations between insects and Apiaceae (Berenbaum 1990) noted that records of apiaceous feeders or their relatives on araliaceous hosts were quite rare. Besides Molytini, another New Zealand curculionid group (Stephanorhynchus, Eugnominae) has species-groups host specific to Apiaceae, Araliaceae, Pittosporaceae, or Asteraceae (Hudson 1934, Styles 1973, May 1987b). Species-groups of Lepidoptera in Xyridacma (Geometridae), Acrocerops (Gracillaridae), and Pterophorus (Pterophoridae) are found on Araliaceae and Pittosporaceae, with distinct species associated with each family (Dugdale 1975).

Vicariant distribution and sympatric occurrences. The major clades *Hadramphus* and *Lyperobius* are almost totally vicariant, and their distributions overlap only at the southernmost limit of distribution, on tiny Broughton Island in the subantarctic Snares group. These two taxa do occur in geographical proximity in Canterbury, but exhibit ecological vicariance along an altitudinal gradient, with *H. tuberculatus* known from lower altitudes than *Lyperobius* species.

Members of the *L. hudsoni* species-group (*L. barbarae*, *L. hudsoni*, *L. montanus*, *L. townsendi*) and the *L. coxalis* species-group (*L. australis*, *L. coxalis*, *L. nesidiotes*) are all vicariant. Putative closest relatives *L. patricki* and *L.*

Table 2 Numbers of ancestral nodes in the phylogenetic tree separating vicariant and sympatric clades.

Clade	Ancestral nodes (n)
(1) Vicariant	
H, spinipennis-H.stilboco	urpae 1
H. pittospori-H. spinipen	nis/H. stilbocarpae 1
H. tuberculatus-H. pittos	pori/H. spinipennis/H.
stilbocarpae	1
L. carinatus-L. clarkei	ı
L.glacialis-all other Lype	robius 2
L. fallax-L. hudsoni spp.i	L. eylesilL. spedenii spp.lL.
coxalis spp.	1
L. coxalis-L. australis/L.	nesidiotes 1
L. australis-L. nesidiotes	l
(2) Sympatric	
H. stilbocarpae-L. nesidi	otes 12
L. carinatus-L.huttoni	3
L. carinatus-L. spedenii	6
L. clarkei-L. fallax	3
L, carinatus-L. fallax	3
L. huttoni-L. fallax	3
L, hudsoni sppL. speder	iii spp. 3

spedenii are also vicariant, the former species occurring on North Otago and South Canterbury mountains and ranges, the latter on Central Otago and Otago Lakes mountains and ranges and the Takitimu Mountains. Other vicariant patterns of disjunction include the sister species *L. clarkei* (northwest Nelson and Buller ranges) and *L. carinatus* (Seaward Kaikoura Range to mid Canterbury), and the sister-group relationship of *L. fallax* (northern South Island ranges, with southern limits north of the Rakaia River) to a clade comprising *L. coxalis*, *L. hudsoni*, and *L. spedenii* species-groups plus *L. eylesi* (southern South Island and The Snares, with *L. spedenii* extending northwards to just south of the Rakaia River) (Craw 1990).

Vicariant distributions are most common between closely related clades and species, with an average of 1.12 ancestral nodes separating vicariant taxa in the phylogenetic tree. Sympatric occurrences are usually between much more distantly related taxa, with an average of 4.7 ancestral nodes separating those taxa that occur together (Table 2). Sympatry, due to dispersal, is thus secondary to vicariance in these two genera.

Elevational range, habitat, and biogeographic history.

Tectonic and other geological activity tends to result in irregular land surfaces. These irregularities promote biological diversification by changing environments and separating or joining habitats. Tectonic processes leading to

uplift, subsidence, and horizontal displacement along fault zones are postulated to be responsible for the fragmentation of ancestral New Zealand molytine populations, leading to vicariant differentiation at generic and specific levels.

Repeated episodes of uplift and subsidence, and marine transgression and regression, have characterised the geological history of New Zealand since the Mesozoic era. Mountain ranges have been a prominent feature of local landscapes since those times. Published paleogeographic maps illustrate mountainous landforms in what is now southern Nelson/north Westland, east Otago, and Fiordland during Lower Cretaceous time. It is often stated that the extensive New Zealand microcontinent had been eroded to an expansive peneplain surface by the late Cretaceous, but the description 'peneplain' is problematic. Beneath the very late Cretaceous Pakawau coal measures surface relief was at least 100 m over very short distances. Similar relief, though less steep, is known from beneath Eocene coal measures in southwest Nelson and around Huntly (Waikato). In north Westland, the Cretaceous Porarari Group is thought to have been laid down during a period of intense local tectonic activity, and the source of the breccia was probably at a considerable altitude. There was a general tendency for continuing uplift until the end of the Rangitata Orogeny in the late Cretaceous (Suggate et al. 1978).

No epoch of the Cenozoic era lacks deposits indicative of tectonic movement somewhere in New Zealand. During the Paleocene to Late Eocene there was a land of generally low relief flanked by large, low-lying lagoon areas in parts of the eastern South Island, with localised hill and mountain ranges. Late Eocene ranges existed to the north and south of the Manapouri region. Minor mid-Cenozoic uplift affected the western edge of the shelf region in the southern South Island, from the Longwood Range in the south through the Takitimu Mountains to the Bob's Cove area (Lake Wakatipu region) in the north. Early Oligocene and mid Miocene ranges occurred in the Takitimu area. In Otago, the Moonlight Fault is bordered by a discontinuous narrow strip of Oligocene beds, interpreted as a tectonic zone active during Oligocene sedimentation and Kaikoura deformation (Norris & Turnball 1993).

Initiation of the Kaikoura Orogeny, which gave rise to the present-day axial ranges, can be placed with reasonable confidence in Early Miocene time for many parts of New Zealand. The modern Southern Alps may have developed northwards from an embryonic mountain range in north-west Otago originating through significant late Oligocene - early Miocene uplift (Craw 1995). A distinct period of early Miocene uplift occurred in Marlborough (Baker & Seward 1996), and middle to late Miocene uplift

is reported from South Westland (Sutherland 1996). In many parts of New Zealand the uplands form disjointed and faulted blocks, remnants of ancient coastal plains, which have been uplifted to their present position.

Evolutionary and ecological differentiation of the alpine biota is closely linked to these earth history events. Rocky and other coastal, insular, lowland, and alpine habitats are ecologically similar. Not only are there ecological correlations between these environments but also historical ones. Many montane, subalpine, and alpine species have coastal, insular, or lowland disjunct populations or vicariant relatives. Coastal, insular, and alpine biota are ecologically and historically homologous (Heads 1990).

Most Lyperobius species occur in higher montane, subalpine, and alpine grassland, herbfield, and rocky places in the South Island. Lyperobius huttoni has a wider tolerance in elevational range than other species, with populations at low altitude on the southern Wellington coast, montane in the Hunters Hills (South Canterbury), and subalpine on several South Island ranges east of the main divide. The southernmost species, L. nesidiotes, is confined to a small islet in the subantarctic Snares islands.

In contrast, *Hadramphus* species have a strictly coastal, insular, and lowland elevational range (Text-fig, 5). This genus appears to have been more widely distributed in the past, as Dr T. Worthy has recently discovered a large *Hadramphus* specimen in a subfossil deposit on the west coast of the South Island (Te Ana Titi cave, Fox River, 12 Mar. 1992 – NZAC). No large molytine species is known at present to inhabit this area. This subfossil specimen resembles a large female *Hadramphus* in NZAC collected at Puysegur Point, and identified below as *H. stilbocarpae*. In light of this discovery the Puysegur Point population of *Hadramphus* argently requires specialist study, since it and the subfossil material may represent a fifth, as yet undescribed, *Hadramphus* species.

It has been suggested that some ancestral alpine plant species of ancient mountains could have survived on 'rocky faces' or in habitats characterised by cool, wet, infertile old soils at low altitudes during the early to mid Cenozoic, and later given rise to the present alpine tlora (Cockayne 1928, Wardle 1968, 1978). Particularly relevant is the fact that numerous species of the probable ancestral host-plant family and genera (Apiaceae: Aciphylla and Anisotome) occupy coastal cliff and lowland peaty and swampy habitats today (Dawson 1971).

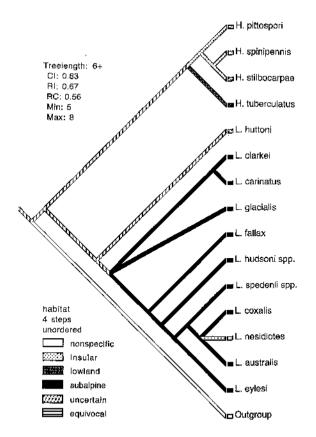
Insular and coastal weediness characterised Mesozoic weevil taxa ancestral to modern forms. The New Zealand Molytini are hypothesised to have descended from a Late Cretaceous - early Tertiary brachypterous ancestral complex distributed in coastal insular and lowland sites, and on mountain ranges. That the common ancestor of *Had-*

Table 3 Taxonomic root weight values for *Hadramphus* and *Lyperobius* species and species groups.

Тахоп	Information	Quotient	Weight	Percentage
H. pittospori	3	24.6	3	8.81
H. spinipennis	4	18.5	2.26	6.64
H. stilbocarpae	4	18.5	2.26	6.64
H. tuberculatus	2	37	4.51	13.2
L. huttoni	2	37	4.51	13.2
L. clarkei	4	18.5	2.26	6.64
L. carinatus	4	18.5	2.26	6.64
L. glacialis	3	24.6	3	8.81
L. fallax	4	18.5	2.26	6.64
L, hudsoni spp.	5	14.8	1.8	5.3
L. spedenii spp.	7	10.6	1.3	3.8
L. coxalis	8	9.25	1.13	3.3
L. nesidiotes	9	8.2	1	2.9
L. australis	9	8.2	1	2.9
L. eylesi	6	12.3	1.5	4.4

Table 4 Summed percentage taxonomic diversity values (TDV) for selected critical areas where two or more *Hadramphus* and/ or *Lyperobius* species are sympatric. Areas ranked for importance by this measure.

Area	TDV	Rank	
Black Birch Ra.	19.8	l =	
Craigieburn Ra,	19.8	1=	
Seaward Kaikoura Ra.	19.8	1=	
NW Nelson/Buller	13.3	2=	
Broken River Basin	13.3	2=	
Murchison Mtns	13	3	
The Snares islands	9.5	4	
Garvic Mtns	9.1	5=	
Takitimu Mtns	9.1	5=	
North Otago mtns	9.1	5≖	
The Remarkables	9.1	5≂	



Text-fig. 5 Distribution of habitats mapped onto majority rule consensus tree for *Hadramphus* and *Lyperobius*.

ramphus and Lyperobius was flightless is a reasonable hypothesis on the basis of parsimony, since all extant species of these genera are brachypterous and flightless. Widespread ancestral populations were subjected to phases of 'modernization' during which tectonic displacement, subsidence, and uplift disrupted and fragmented them, with subsequent differentiation at the generic and specific levels.

CONSERVATION STATUS AND VALUE

Large weevil species are generally considered in New Zealand conservation biology (e.g., Ramsay et al. 1988, Thomas 1996) to be at threat from introduced rodent predators. There is some anecdotal and empirical evidence supporting this supposition. Bull (1967) provided evidence that mice prey upon L. huttoni adults, and Kuschel (1971) attributed the absence of H. stilbocarpae on Big South Cape Island - where it was once present - to predation by rats. While rodents undoubtedly prey on these weevils, other factors such as habitat degradation and destruction due to agricultural practices, reduction in the size and extent of host plant populations through browsing by stock and wild goats (Meads 1990), and even removal of the entire habitat through quarrying (which happened to a viable population of L. huttoni at Owhire Bay, south Wellington coast) pose just as great a threat as rodents to populations of these endangered flightless species. Rodents may also compete for host plants with these weevils, as Roberts (1895) has noted that introduced rats feed on the roots of Aciphylla,

In 1980 H. spinipennis, H. stilbocarpae, H. tuberculatus, and L. huttoni were added to the protected fauna list in the Seventh Schedule of the Wildlife Amendment Act 1980. Being taxonomically and ecologically diverse, individually habitat specific, phytophagous on specific host genera, and easily identified, these relatively large weevils would seem to be an ideal biological indicator group for the purposes of conservation and environmental assessment.

There is increasing interest in utilising phylogenetic hypotheses as measures of biodiversity in prioritising, ranking, and targeting species for 'conservation value' (e.g., Williams *et al.* 1991, 1993, Faith 1994, Humphries *et al.* 1995). Application of the taxonomic root weighting method (Williams *et al.* 1991) to the phylogenetic tree provides a means of assigning quantitative values for each species or species-group in that tree (Table 3).

Fortuitously, root weighting analysis indicates that, given the present situation and current legislation, protection of these endangered, rare, and vulnerable species covers 39.68% of total taxonomic diversity of New Zealand Molytini. According to this method the next taxon that should be added to the protected fauna list is either H. pittospori or L. glacialis. Addition of either one or other of these taxa would bring protected taxonomic diversity coverage up to 48.49% of total taxonomic diversity for this group. Nearly 50% of total taxonomic diversity would therefore be protected by listing only 25% of species in this clade. Since three Hadramphus species are already on the list, it would be more desirable to conserve L. glacialis to maximise the number of clades protected. Root weight values can also be combined with information from geographic distribution, to identify and rank 'critical areas' for biodiversity preservation, by summing the percentage taxonomic diversity values for a selection of areas where two or more species occur (Table 4).

In setting conservation priorities taxonomic root weighting gives much higher weights to earlier diverging, basally branching taxa (Humphries *et al.* 1995). While there are sound reasons for assigning high conservation priority to taxa basal within their lineages (Stiassny & de Pinna 1994), weighting methods that emphasise their speciesrich sister clades also deserve consideration. An alternative approach is to attempt to conserve taxa that may be able to support further evolution. This is the methodology advocated by Erwin (1991), who suggests that members of rapidly evolving clades or 'evolutionary fronts' have more potential to lead to future diversity than species-poor lineages. As basal lineages of New Zealand Molytini are species poor and have already received a much higher weighting in conservation prioritisation and legal

protection, consideration should be given to protecting some of the more speciose high-altitude *Lyperobius* clades. Rather than adding a further early diverging species to the protected list, members of the montane to subalpine *L. coxalis*, *L. hudsoni*, or *L. spedenii* speciesgroups could be granted consideration as the next conservation priority. Placing priority on one or more of these speciose clades would also maximise the diversity of habitats occupied by the conserved species. At present most conservation effort and legislation are focused on basal lineages inhabiting coastal, lowland, and insular habitats.

DESCRIPTIONS

Genus Hadramphus Broun

Hadramphus Broun, 1911: 104–105. –Hudson 1923: 390.
–Schenkling & Marshall 1931: 18. –Hudson 1934: 214. –Kuschel 1971: 240. –May 1971: 293.

Type species *Hadramphus spinipennis* Broun, 1911, by original monotypy.

Karocolens Kuschel, 1987: 15, new synonymy.

Type species Karocolens pittospori Kuschel, 1987, by original designation.

Redescription. Length 11.7–23 mm, width 6.5–11.5 mm. Prothorax with ocular lobes well developed and covering eyes. Pronotum with 4 discal tubercles and 1 or 2 lateral tubercles. Elytral intervals 3, 5, and 7 with tubercles. Mesepisternum with a distinct clongate impression. Metasternum in front of hind coxae with a well developed projecting tooth.

Remarks. When describing *Karocolens*, Kuschel (1987: 15–16) wrote as follows.

"Closely related to *Hadramphus* Broun but differing in the following main characters.

Frons with large impression. 2nd segment of funicle roughly as long as 1st. Club segment 1 slender, nearly stalked at base, widening in straight line. Prothorax as or nearly as long as wide, diverging in straight line to anterior third, with large triangular knob at this point and a small one behind. Elytra widening in straight line to anterior third, with small tubercle or swelling on the basal angles, with 1 or 2 posthumeral tubercles on interstria 9. Femora armed with tooth; tibiac sinuous on lower edge, with distinct premuero in both sexes.

"MALE: Tegmen with a pair of teeth on anterior margin of ring and broad parameres. Aedeagus with thick, permanently lifted ostial valves; floor of internal sac without sclerite beyond ostium at aedeagal apex.

"FEMALE: Tergal pouches at basal angles of 8th tergite present, large, bearing filamentous prokaryotes (bacteria). Hemisternal pouches long."

Some of the characters listed as distinguishing *Karocolens*, though, are shared with *Hadramphus* species. For instance, *H. spinipennis* has a femoral tooth that is visible in specimens without the assistance of any magnification, and all *Hadramphus* species have a premucro in both sexes. Other characters shared with *Hadramphus* are present even though they are stated to be absent in *Karocolens*. In the male genitalia of *K. pittospori* the endophallus has a pair of sclerites embedded in the membranous floor, beyond the ostium, at the aedeagal apex which appear to be homologous with the single inverted V-shaped sclerite found in other *Hadramphus* species.

Although a number of unique characters (within the clade comprising the New Zealand Molytini) remain that phenetically separate *H. pittospori* from other *Hadramphus* species, phylogenetic analysis demonstrates that this species belongs to a clade comprising (*H. tuberculatus* + (*H. pittospori* + (*H. spinipennis* + *H. stilbocarpae*))) (see Text-fig. 1). If formal classification is to be as isomorphic as possible with reconstructed genealogy (e.g., Darwin 1859, Hennig 1966, Nelson 1973), it is more informative to recognise two genera only in New Zealand Molytini, and to synonymise the monotypic genus *Karocolens* under *Hadramphus*. Immature stages support this synonymy. May (1987: 30) notes: "The larva and pupa of *K. pittospori* exhibit only minor difference from the immature stages of *H. stilbocarpae* and from those of *Lyperobius* Pascoe."

Hadramphus pittospori (Kuschel) new combination

Figures 1, 44, 45, 48; Map 1

pittospori Kuschel, 1987: 15-18 (Karocolens). -May 1987a: 29-34.

Type data. Holotype: male, ND, Poor Knights Islands, Aorangi, 15 December 1981, reared from *Pittosporum crassifolium* wood collected 1 month earlier, J.C. Watt (NZAC), 19.7×8.5 mm.

Paratypes (6 male, 6 female); listed in Kuschel (1987).

Redescription. Length 16.5–19.7 mm, width 7.5–8.5 mm. Integument dark brown to blackish brown; body vestiture of elliptic to lineal-lanceolate scales, densest on dorsal surface, the scales yellowish on sides of dorsal surface and reddish-brown to cinnamon on median areas of pronotum and elytra and on elytral declivity. Rostrum relatively

long, 2.26–2.49× its apical width. Head with a distinct impression between eyes. Funicle with first 2 segments subequal in length, Antennal club with 1st segment elongate, almost stalked at base. Pronotum (including lateral tubercles) as long as wide or nearly so, widest at apical third, sparsely granulate, with 4 discal tubercles and a median carina between anterior tubercles. Pronotum laterally with a large triangular knob at apical third and a small median knob. Elytra elongate, widening in a straight line to apical quarter, with a humeral tubercle; interval 5 with 3 or 4 tubercles on apical three-fifths, interval 9 with 1 or 2 posthumeral tubercles and an apical tubercle just above articulation of ventrites 4 and 5. Femora armed with a small tooth.

Male. Tegmen with a pair of teeth on anterior margin of ring; parameres broad (Fig. 45). Aedeagus with a short, stout median lobe and thick, permanently raised ostial valves; apodemes longer than median lobe. Endophallus with a pair of sclerites beyond ostium at aedeagal apex; basal sclerite heavily sclerotised on anterior half, less sclerotised and with vestiture on posterior half (Fig. 48).

Female, Hemisternal pouches long, Spermathecal duct not reaching past end of bursa.

Material examined. Type series only (AMNZ, MONZ, NZAC).

Distribution. ND: Poor Knights Islands (Aorangi, Ta-whiti Rahi).

Host plant. Pittosporum crassifolium (Pittosporaceae).

Remarks. This distinctive species, or an as yet unknown sister species, may exist in coastal lowland forest in the North Island and the Marlborough and Nelson areas of the South Island, as well as on offshore islands where woody Pittosporaceae or Araliaceae occur.

Hadramphus spinipennis Broun

Figures 2, 49; Map 2

spinipennis Broun, 1911: 105-106 (Hadramphus). -Hudson 1923: 390. -Kuschel 1971: 240.

Type data. Lectotype: male (here designated), Chatham Islands, "Pitt Is." [T. Hall] (BMNH), 20.6×10 mm. There is one specimen of this species in the Broun Collection (BMNH) and none in the duplicate Broun Collection (NZAC). The original description indicates that Broun had more than one specimen when he described this species, hence the lectotype designation.

Redescription. Length 20.2–23 mm, width 9.6–11.5 mm.

Integument dark reddish-brown; body vestiture of pale yellowish to dark brown, lineal-lanceolate, appressed scales and hairs, densest on dorsal surface. Pronotum with lateral lines and median apical and basal streaks of pale yellowish scales. Rostrum relatively long, 2.3–2.6× its apical width. Funicle with 1st segment 1.5–1.72× as long as 2nd segment. Pronotum (including lateral tubercle) wider than long. Elytra oblong-ovate; tubercles on intervals 3 and 5 conical, on interval 7 spinose; interval 9 with a tubercle just above articulation of ventrites 4 and 5; declivity with a median tubercle on interval 3.

Male genitalia. Median lobe stout; aedeagal apodemes approximately as long as median lobe. Endophallus apex with an inverted U-shaped sclerite (Fig. 49).

Female genitalia. Sternite 8 elongate; apodeme long. Hemisternites with proximal portion noticeably broadened; hemisternal pouch moderately long.

Material examined. Lectotype, plus 21 non-type examples (BMNH, NZAC).

Distribution. Chatham Is: Mangere L., Pitt I., Rangatira (South East) I.

Host plant. Aciphylla dieffenbachii (Apiaceae).

Remarks. The conservation status of *H. spinipennis* has been evaluated by Emberson & Marris (1994) and Emberson *et al.* (1996). It would be worth scarching for this endangered and legally protected species on other islands in the Chathams archipelago. For instance, it has never been recorded on Rekohu (the main island), but could well occur there on the southern coastal cliffs, as well as at higher elevations on the Southern Tableland, where populations of a possible alternative host plant, *Aciphylla traversii*, occur. Population dynamics of this species have been studied by Schöps *et al.* (1998). A colour photograph of this species appears in Dugdale & Emberson (1996: 97).

Hadramphus stilbocarpae Kuschel

Figures 3, 29, 32, 38, 39, 46, 47, 50; Map 3 stilbocarpae Kuschel, 1971: 240 (Hadramphus). –May 1971: 293; — 1981: 269.

Type data. Holotype: male, SI, Big South Cape Island, Murderers Cove, 4 January 1955, R.K. Dell & B.A. Holloway (NZAC), 17×8.7 mm.

Paratypes: listed in Kuschel (1971).

Redescription. Length 15.5-21.7 mm, width 7.8-9.5 mm.

Integument dark brown; vestiture of greyish-brown to dark brown, appressed, lineal-lanceolate scales covering body; scales on top of tubercles paler. Pronotum with lateral and median pale lines; lateral lines often extending back onto elytral interval 5. Rostrum relatively long, 2.4–2.7×its apical width, usually with a weak median carina or smooth line. Funicle with 1st segment 1.4–1.7× as long as 2nd segment. Pronotum (including lateral tubercles) 1.15–1.35× wider than long, with distinct discal knobs; surface granulose to granular rugose. Elytra clongate ovate, with surface granulate; interval 7 with conical tubercles, interval 9 with a tubercle just above articulation of ventrites 4 and 5; declivity with a median tubercle on interval 3.

Male. Median lobe short, stout; aedeagal apodemes shorter than median lobe. Endophallus apex with an inverted U-shaped sclerite (Fig. 50).

Female. Sternite 8 with apodeme long. Hemisternites with proximal portion noticeably broadened; hemisternal pouches long.

Material examined. Type series, plus 160+ non-type examples (AMNZ, BMNH, CMNZ, MONZ, NZAC, OMNZ).

Distribution. FD: Breaksea Is, Breaksea Sound; Resolution I. (exposed outer coast and Five Fingers Peninsula); Puysegur Point. **SI**: Bird I. (Fouveaux Strait); Big South Cape I. **The Snares** (North East I., Broughton I.).

Host plants. Anisotome lyallii (Apiaceae); Stilbocarpa lyallii, S. robusta (Araliaceae).

Remarks. Larvae and pupae have been described by May (1971, 1981). Colour photographs of an adult and its habitat, along with valuable notes on behaviour and ecology, can be found in Meads (1990). In addition, *H. stilbocarpae* has been illustrated and discussed by Rance & Patrick (1988), Morris & Hayden (1995), Peat & Patrick (1996), and Close (1997). Translocation efforts and other aspects of conservation management of this species have been reported by Thomas *et al.* (1992), Meads (1994), and Thomas (1996).

Hadramphus tuberculatus (Pascoe)

Figures 4, 51; Map 4

tuberculatus Pascoe, 1877; 142 (Lyperobius), -Broun 1880; 445. -Hudson 1923; 390. -Dalla Torre, Schenkling, & Marshall 1932; 66. -Kuschel 1971; 240 (Hadramphus).

Type data. Lectotype: male (here designated), MC, "Christchurch" [C.M. Wakefield] (BMNH), 14.5×7.5 mm.

Redescription. Length 11.7–16.3 mm, width 6.5–8.3 mm. Integument dark brown; body vestiture of greyish-brown, appressed, lineal-lanceolate scales, those on head, elytral intervals, and top of tubercles paler. Pronotum with pale lateral and median stripes on basal half. Rostrum relatively long, 2.0–2.16× its apical width. Funicle with 1st segment 1.46–1.8× as long as 2nd segment. Pronotum (including lateral tubercles) 1.13–1.39× wider than long, with 4 low discal elevations. Elytra oval, widest near middle, with surface granulate; interval 3 with 3 low flat elevations, the basal one almost costate, the others tuberculate; interval 5 with 2 mid-discal, low, flat, tuberculate elevations; interval 7 with 3 low, flat, tuberculate elevations; declivity without tubercles on intervals 3 and 9.

Male. Median lobe stout; aedeagal apodemes a little shorter than median lobe. Endophallus apex with an inverted U-shaped sclerite (Fig. 51).

Female, Sternite 8 elongate; apodeme long. Hemisternites with proximal portions noticeably broadened; hemisternal pouches short.

Material examined. Lectotype, plus 16 non-type examples (BMNH, CMNZ, NZAC).

Distribution. NC, MC, SC: Canterbury plains, foothills, and fringing ranges — Oxford, Christchurch, Blackford and Mt Oakden (Rakaia R.), Temuka, Waimate.

Host plants. Probably *Aciphylla subflabellata* and *A. glaucescens* (Apiaceae).

Remarks. This legally protected species is possibly extinct (last specimen collected Waimate, 1922). It is mentioned in important conservation publications as having once occurred on Banks Peninsula (e.g., Wells et al. 1983, Ramsay et al. 1988, Tisdall 1994). This distribution information is based on Kuschel (1971: 240), who noted "H. tuberculatus... is known mainly from Banks Peninsula but was found as far south as Waimate." None of the known specimens bears a locality label 'Banks Peninsula' nor any label data that could possibly be interpreted as indicating collection there. The nearest recorded specimens to Banks Peninsula are from Christchurch, including the type series, of which Pascoe (1877; 142) wrote: "Hab. Christchurch ... found on a plant called the 'Spaniard' [i.e., Aciphylla]."

Early accounts of the indigenous vegetation around Christchurch contemporaneous with the collection of the type series (e.g., Travers 1869, Armstrong 1870) record the presence of Aciphylla species in a variety of habitats, including sandhills, swamps, and plains. These host plants for *H. tuberculatus* have been recorded from Hagley Park (near the centre of Christchurch) as late as 1905 (Herriott 1919), and the last record of this weevil in Christchurch was in 1910. Distribution data from known specimens extends from Waimate and Temuka in eastern South Canterbury to Oxford in southern North Canterbury, with western and eastern limits at Mt Oakden and Christchurch respectively. Subfossil records of this species from South Canterbury (Worthy 1997) do not represent significant extensions to the known range.

Genus Lyperobius Pascoe

Lyperobius Pascoe, 1876: 54. –Broun 1880: 445. –Hutton 1904: 203. –Hudson 1923: 390. –Dalla Torre, Schenkling, & Marshall 1932: 65. –Hudson 1934: 133. –Kuschel 1971: 239; — 1987: 15. Type species Lyperobius huttoni Pascoe, 1876, by original monotypy.

Redescription. Length 11.5–28 mm, width 6–12.7 mm. Prothorax with ocular lobes slightly developed. Pronotum not tuberculate, its sides subparailel to broadly rounded, without lateral knobs. Elytra not tuberculate; intervals flat, convex, or costate. Mesepisternum with no distinct impression, at most with a few confluent punctures. Metasternum in front of hind coxae with at most a prominent overhang.

Lyperobius australis new species

Map 5

Type data. Holotype: female, FD, Mt Inaccessible, 3400 ft [1020 m], 5 February 1985, A. Frampton (NZAC), 23×9.7 mm.

Paratypes: I female, FD, near Lake Fraser, Fcb 1983, A.E. Frampton.

Description. Length 20.5–23 mm, width 9.2–9.7 mm.

Integument black to dark reddish-brown; body vestiture sparse, of pale yellowish-white scales, densest on head and pronotum, as narrow stripes between elytral striac and costate intervals, and on upper inner face of all coxae. Rostrum relatively long and thin, 2.0-2.05× its apical width. Funicle with 1st segment 1.6-1.66× as long as 2nd segment; segments 3-6 about as long as broad; 7th seg-

ment transverse. Pronotum transverse, 1.2–1.25× wider than long, with sides broadly rounded; disc with a median, elongate, low, flat, smooth area and a distinct basal impression. Elytra elongate elliptic, with even and uneven elytral intervals raised as distinct costac; intervals 3 and 9 costate and conjoint on elytral declivity. Coxae with a dense scale patch on upper inner face.

Male, Unknown.

Female. Ventrite 5 very convex in basal half, with a medio-apical longitudinal impression and upturned apical margin. Sternite 8 broad; apodeme long and thin. Hemisternites with stout setae on distal portion; hemisternal pouches short, broad.

Material examined. Type specimens only (NZAC).

Distribution. FD: mountain ranges between Edwardson Sound and Dusky Sound (e.g., Kakapo Ra.).

Host plant. Probably an Anisotome species (Apiaceae).

Remarks. Lyperobius australis is easily distinguished from its closest relatives (L. coxalis and L. nesidiotes) by the combination of elytra elongate elliptic, pronotal sides broadly rounded, elytral intervals 3 and 9 costate and conjoint on declivity, and female 5th ventrite with basal half very convex.

Lyperobius barbarae new species

Figures 18, 30, 52,70, 77; Map 6

Type data. Holotype: female, MK, Mt Sutton [west of Lake Ohau], 6000 ft [1800 m], 29 November 1960, M. Fitzgerald (OMNZ, ex R.C. Craw coll.), 20.8×9.7 mm.

Paratypes: 2 males, 2 females, MK, Ohau Ski Field, 31 Dec 1988, B.H. Patrick.

Description. Length 16.7–20.8 mm, width 8.5–9.7 mm. Integument black to dark reddish-brown; body vestiture of pale whitish-yellow to white, oval to ovate scales, densest on lateral margins of pronotum and elytral intervals 2, 4, and 6. Rostrum relatively long and thin, 2.23–2.45× its apical width. Funicle with 1st segment 2× as long as 2nd segment; segments 3–7 distinctly transverse. Pronotum 0.95–0.98× as long as wide, with sides gently rounded, subparallel on basal half; disc with diffuse and indistinct lateral and median sulci, these sometimes obsolete or obsolescent, and a distinct medio-basal impression (Fig. 18). Elytra clongate ovate; intervals 3, 5, and 7 raised as costae; interval 9 raised as costae on apical third and conjoint with interval 3 on declivity. Tarsal segments 1

and 2 with apical sole hairs longer than those on segment 3, and greatly projecting distally.

Male. Ventrite 5 with a distinct medio-apical impression. Median lobe stout; aedeagal apodemes about as long as median lobe. Endophalfus with basal sclerite bearing lateral apical processes; apex with a pair of sclerites (Fig. 52).

Female. Ventrite 5 convex on basal half, with distinct lateral impressions. Sternite 8 elongate; apodeme long (Fig. 70). Hemisternites with abundant long, fine setae on distal portion; hemisternal pouches relatively short to short. Bursa copulatrix with a distinct, broad, selerotised area near junction with oviduct (Fig. 77).

Material examined. Type series, plus 22 non-type examples (BHPC, BIPB, NZAC, OMNZ).

Distribution. MK, SC, CO, DN: Mt Sutton, Ben Ohau Ra. (southern end), St Mary's Ra., Hawkdun Ra., Ida Ra., Kakanui Mtns.

Host plants. Aciphylla dobsonii, A. flexuosa, A. montana var. gracilis (Apiaceae).

Remarks. Lyperobius barbarae is easily distinguised from its closest relatives L. hudsoni and L. townsendi by its much less developed, more diffuse and indistinct sulci and scale pattern on the pronotal disc (cf. Fig. 18, 21, 24). A colour photograph can be found in Patrick (1991, fig. 9).

This distinctive species is named for Dr Barbara Barratt, whose entomological research in the southern South Island mountains has contributed greatly to this revision.

Lyperobius carinatus Broun

Figures 53, 71, 78; Map 7

carinatus Broun, 1881: 702 (Lyperobius). –Hutton 1904: 203. –Hudson 1923: 390. –Dalla Torre, Schenkling, & Marshall 1932: 65. –Hudson 1934: 214.

Type data. "No locality, came from J.D. Enys, Esq." (CMNZ), 20.4×9.2 mm.

This specimen bears two 19th century labels reading "carinatus" [in Broun's hand] and "J.D.E." It matches the original description, and has been labelled "Holotype female, *Lyperobius carinatus* Broun, 1881, R.C.Craw det. 1997."

Redescription. Length 20.4–24.8 mm, width 8.6–10.8 mm

Integument reddish-brown to black; body vestiture of orbicular to elongate, lineal-lanceolate, white or yellowish

white scales, densest on base of head, sides of pronotum, and elytral intervals 2, 4, and 6. Rostrum short and thick, 1.5–1.7× apical width in length. Funicle with 1st segment 1.5–1.8× as long as 2nd segment. Pronotum transverse, 1.1–1.25× wider than long, with sides strongly rounded; disc with a median basal impression. Elytra elongate elliptic; intervals 3, 5, and 7 strongly costate; interval 9 costate on apical quarter; interval 8 flat on basal and apical quarters, raised medially; intervals 2, 4, and 6 flat, coarsely granulate.

Male. Ventrite 5 with a distinct medio-apical impression. Median lobe short and stout; aedeagal apodemes shorter than median lobe. Endophallus with a distinct, inverted V-shaped apical sclerite; basal sclerite without distinct latero-apical arms (Fig. 53).

Female. Ventrite 5 slightly convex basally, with a shallow impression. Sternite 8 with apodeme short and broad (Fig. 71). Hemisternites stout, broad, styli short, broad, inserted apico-laterally; hemisternal pouches very long (Fig. 78).

Material examined. Holotype, plus 21 non-type examples (BMNH, CMNZ, LUNZ, NZAC).

Distribution. KA, MC, SC, MK: mountain ranges — Seaward Kaikoura Ra. (Kahutara Saddle), Craigieburn Ra., Broken R. Basin, Mt Temple, Jollie Peak, Mt Hutt, Mt Somers, Carney's Creek, McCoy's Creek (upper Rangitata R.), Mt Cook National Park, Mt Dalgety.

The Kahutara Saddle record is taken from Hunt (1996); no specimens from this area have been examined by the author. Specific status of northeastern South Island *Lyperobius* populations require specialist assessment as there may be undescribed taxa in this area.

Host plants. Aciphylla species (Apiaceae).

Remarks. Although one of the earliest described species, *L. carinatus* is very poorly represented in collections. Its distributional limits and population status should be ascertained, as this species – found in the drier and environmentally degraded mid-eastern South Island mountain ranges – may be endangered.

Lyperobius clarkei new species

Figures 5, 11-14, 40, 41; Map 8

Type data. Holotype: female, NN, Mt Arthur, 5000 ft [1500 m], 4 February 1965, J.I. Townsend & A.K. Walker, *Aciphylla ferox* (NZAC), 25.1×11.8 mm.

Paratypes: 2 females, same data as holotype; 3 males, NN, Mt Arthur, 5000 ft [1500 m], 15 December 1961, J.I. Townsend & G.F. Woods.

Description. Length 20.5–28 mm, width 9.2–12.2 mm.

Integument black; body vestiture of pale yellowish-white, lineal-lanceolate scales, densest on head and sides of pronotum, and forming stripes on clytral disc, declivity, and sides; secondary scale stripes also present. Rostrum short and thick, 1.6–1.9× as long as apical width. Funicle with 1st segment 1.6–1.78× as long as 2nd segment (Fig. 14). Pronotum transverse, 1.15–1.2× wider than long, with sides gently to strongly rounded, a median, smooth, raised area, and a basal impression. Elytra elongate elliptic; intervals 3, 5, and 7 strongly costate; secondary costate on intervals 2 and 4 vestigial to strongly developed, and on interval 6 absent, vestigial, or strongly developed.

Male. Ventrite 5 with an indistinct medio-apical impression (Fig. 40). Median lobe stout; aedeagal apodemes shorter than median lobe. Endophallus with apical selerites; basal sclerite with apico-lateral processes (Fig. 54).

Female. Ventrite 5 with an indistinct medio-apical impression (Fig. 41). Sternite 8 truncate apically; apodeme long. Hemisternites stout, broad; styli short, broad, inserted apicolaterally; distal plate with a rod-like proximal extension; hemisternal pouches long.

Material examined. Type series, plus 158 non-type examples (AMNZ, NZAC).

Distribution. NN, BR: mountain ranges – Arthur Ra., Domett Ra., Marino Mtns, Braeburn Ra., Matiri Ra., Glasgow Ra.

Host plant. Aciphylla ferox (Apiaceae).

Remarks. Lyperobius clarkei is readily distinguishable from its sympatric congener L. fallax by size, extensive development of secondary costae, and genital characters. Vicariant populations show consistent geographic variation in some external characters. Northern populations from Mt Arthur (Arthur Range) south to Mt Owen (Marino Mountains) are more robust, with strongly rounded pronotal sides and well developed costae in elytral interval 6. Southern populations (e.g., from the Glasgow Range) are slender with gently rounded pronotal sides and the costae in intervals 6 absent to vestigial. The species is named in honour of the entomologist C. E. Clarke.

Lyperobius coxalis Kuschel

Figures 33, 55; Map 9

coxalis Kuschel, 1987; 18 (Lyperobius).

Type data. Holotype: male, FD, Hunter Mountains, Mt Burns, 1300 m, January 1970, J.1. Townsend (NZAC), 19×9.3 mm.

Paratypes (n=121): listed in Kuschel (1987).

Redescription. Length 14-23 mm, width 7.3-11 mm.

Integument black; body vestiture of greyish-white to yellowish-white, orbicular to ovate scales, densest on base of head, elytral intervals 2, 4, and 6, and upper inner face of coxae. Rostrum relatively short and thick, length 1.7–1.8× apical width. Funicle with 1st segment 1.4–1.44× as long as 2nd segment; segments 3–7 transverse. Pronotum transverse, 1.19–1.25× wider than long; disc with an abbreviated median carina or clongate, low, flat, smooth area on apical two-thirds, a shallow median basal impression, and shallow mediolateral impressions. Elytra clongate ovate; intervals 3, 5, and 7 strongly raised as costae; interval 9 costate on apical quarter and conjoint with costae on interval 3; intervals 2, 4, and 6 flat, with sculpture of fine, low granules. Coxae with a distinct, dense patch of slightly raised scales on upper half of inner face (Fig. 33).

Male. Ventrite 5 with a distinct mid-apical impression. Median lobe elongate; aedeagal apodemes distinctly shorter than median lobe. Endophallus with no apical sclerite; basal sclerite without apicolateral processes (Fig. 55).

Female. Ventrite 5 weakly convex basally, with a shallow medio-apical impression and upturned apical margin. Sternite 8 elongate; apodeme relatively long. Hemisternites with stout setae on distal part; hemisternal pouches short.

Material examined. Type series only (AMNZ, BMNH, CMNZ, FRNZ, LUNZ, MONZ, NZAC, OMNZ).

Distribution. FD: mid-eastern to southern ranges from west of L. Te Anau to west of L. Poteriteri (Murchison Mtns, Kepler Mtns, Turret Ra., Hunter Mtns, Heath Mtns, Cleughearn Peak, Kaherekoau Mtns, Cameron Mtns).

Host plants. Aciphylla crosby-smithii, A. lyallii, A. pinnatifida, Anisotome aromatica, A. capillifolia, A. haastii (Apiaceae).

Remarks. Lyperobius coxalis is easily distinguished from sympatric congeners by the distinct dense patch of slightly raised scales on the coxae, and from its closest relatives L. australis and L. nesidiotes by the combination of elongate -ovate elytra, flat elytral intervals 2, 4, and 6, and relatively short and thick rostrum.

Lyperobius cupiendus Broun

Figures 15, 19, 56, 72, 79; Map 10

cupiendus Broun, 1886: 962 (Lyperobius). –Hutton 1904:
 203. –Hudson 1923: 390. –Dalla Torre, Schenkling, & Marshall 1932: 65. –Hudson 1934: 214.

aciphyllae Broun, 1917: 442 (Lyperobius), new synonymy.

Type data. Holotype of *cupiendus*: male, "Mt Tyndall, 6500 ft [1950 m], GM Thomson" (BMNH), 15.6×9.1 mm. Holotype of *aciphyllae*: female, "Garvie Mts, 7-1-1914" (BMNH), 16.8×8.6 mm.

Redescription. Length 12,2–19 mm, width 6,5–9,7 mm. Integument dark reddish brown to black; body vestiture of orbicular to ovate, white to pale yellowish-white scales, densest on base of head, sides and middle of pronotum, and elytral intervals 2, 4, and 6. Rostrum relatively short and thick, length 1,6–1.8× apical width (Fig. 15). Funicle with 1st segment 2× as long as 2nd segment; 7th segment transverse (Fig. 15). Pronotum distinctly transverse, length 0.78–0.9× width, with sides strongly rounded (Fig. 19). Elytra ovate; intervals 3, 5, and 7 distinctly raised as thick, prominent costae; intervals 2, 4, 6, and 8 either flat or partially to fully raised as secondary costae; interval 9 costate and conjoint with interval 3 on declivity.

Male. Ventrite 5 with a distinct, shallow, medio-apical impression. Median lobe stout; aedeagal apodeme longer than median lobe. Endophallus with apical sclerites; basal sclerite with apicolateral processes (Fig. 56).

Female. Ventrite 5 with a distinct medio-apical impression and upturned apical margin. Sternite 8 with apodeme long (Fig. 72). Hemisternites with robust long setae on distal portion; hemisternal pouches short, broad. Bursa copulatrix with accessory lobes (Fig. 79).

Material examined. Holotypes, plus 65 non-type examples (AMNZ, BHPC, BIPB, BMNH, NZAC).

Distribution. CO, OL: mountain ranges to west of L. Wanaka (Cascade Saddle, Mt Aspiring, Mt Tyndall, Headlong Peak, Niger Peak), Pisa Ra., The Remarkables, Old Woman Ra., Kopuwai / Old Man Ra., Carrick Ra., Garvie Mtns, Um-brella Mtns,

Recorded at 1300 m on the Umbrella Mountains (Dickinson 1988).

Host plants. Aciphylla congesta, A. lecomtei, A. pinnatifida, A. simplex, Anisotome flexuosa, A. imbricata (Apiaceae). Remarks. Lyperobius cupiendus is easily distinguished from all other species by the combination of small size, relatively thick rostrum, transverse pronotum, funicle with first segment twice as long as second segment, and orbicular to ovate scales on elytral disc.

Elytral fragments (in OMNZ) collected in the Earnscleugh Cave, at the foot of the Old Man Range, suggest that this species may have once occurred at lower altitudes.

Lyperobius eylesi new species

Figures 27, 57, 58, 73, 80; Map 11

Type data. Holotype: male, FD, Mt Wilmot, 1350 m, Manapouri Exp[edition], Jan[uary] 1970, J. McBurney (NZAC), 17.9×8.5 mm.

Paratypes: 4 females, same data as holotype; 1 male, 4 females, FD, Mt Barber, 1100–1350 m, Manapouri Expledition, Janjuary 1970, J.S. Dugdale.

Description. Length 16.2-24.9 mm, width 8-11.5 mm.

Integument black to dark reddish brown; body vestiture of pale yellowish-white, oval to elongate-ovate scales, densest on head and elytral intervals 2, 4, and 6. Rostrum moderately long and thin, 2–2.1× its apical width. Funicle with 1st segment 1.6× as long as 2nd segment; segments 3–7 rounded. Pronotum transverse, approx. 1.2× as wide as long, with sides broadly rounded and with a distinct, shallow, median basal impression. Elytra elongate ovate; intervals 3, 5, and 7 raised as distinct costac; intervals 2, 4, and 6 flat to slightly raised, granulate, transversely rugose; interval 8 flat; intervals 3 and 9 costate and conjoint on declivity (Fig. 27). Tarsal segments 1 and 2 with sole hairs no longer than those on segment 3, and not greatly projecting distally.

Male. Ventrite 5 with a shallow medio-apical impression. Median lobe short and stout; acdeagal apodemes just shorter than median lobe. Endophallus with an inverted V-shaped apical sclerite; basal sclerite with large, rounded apicolateral processes (Fig. 57).

Female. Ventrite 5 convex on basal half, with a distinct longitudinal impression on apical half; apical margin upturned. Sternite 8 spatulate, elongate; apodeme relatively short (Fig. 73). Hemisternal pouches short. Bursa copulatrix with a sclerite near junction with oviduet (Fig. 80).

Material examined. Type series, plus 8 non-type examples (BHPC, NZAC).

Distribution. FD: Tutoko Vly, Murchison Mtns, Mt Barber, Mt Wilmot, Wilmot Pass (west of L. Manapouri).

Host plants. Aciphylla congesta, Aciphylla sp. (Apiaceae).

Remarks. Lyperobius eylesi is easily distinguished from known allopatric and sympatric congeners by the combination of absence of scale patches on the upper inner face of the coxae, elytral interval 3 strongly costate and conjoint with interval 9 on the declivity, spatulate shape of the female eighth sternite, and male endophallus basal sclerite with broad, rounded apicolateral processes.

Named for Dr Alan Eyles, who pioneered the use of numerical taxonomy in entomological systematics in New Zealand.

Lyperobius fallax Broun

Figures 16, 20, 36, 59; Map 12

fallax Broun, 1917: 443 (Lyperobius). -Hudson 1923: 390. -Dalla Torre, Schenkling, & Marshall 1932: 65. -Hudson 1934: 214.

Type data. Lectotype: female (here designated), MB, "Mt Miromiro, 6000 ft [1800 m], C.Chilton" (BMNH), 15.8×8.0 mm.

Paralectotype: I male (here designated), same data as holotype but with no altitude, 15×7.3 mm.

The female specimen has been designated as lectotype because the original description states "rostrum unimpressed in front of antennae" and "fifth ventral segment unimpressed", which are female characters in this species.

Redescription. Length 13.3-19 mm, width 6.6-9.2 mm.

Integument black; body vestiture of pale yellowish to white ovate scales, densest on pronotal margins and clytral disc and declivity, forming distinct pale stripes on elytra in intervals 2, 4, 6, and 8 and along margin on apical third, with secondary stripes present on declivity. Rostrum relatively thin, 1.95–2.16× apical width in length (Fig. 16). Funicle with 1st segment 1.3–1.5× as long as 2nd segment (Fig. 16). Pronotum transverse, 1.1–1.2× wider than long, with sides strongly rounded (Fig. 20). Elytra elongate ovate; intervals 3, 5, and 7 raised as costae; interval 9 costate on apical quarter and conjoint with interval 3. Tarsal segments 1 and 2 with sole hairs not longer than those on segment 3, and only slighly projecting distally (Fig. 36).

Male. Ventrite 5 with a distinct mid-apical impression. Median lobe stout; acdeagal apodemes about as long as median lobe. Endophallus with apical sclerites (Fig. 59).

Female. Ventrite 5 convex on basal half. Sternite 8 with apodeme short. Hemisternal pouches short.

Material examined. Type specimens, plus 86 non-type examples (AMNZ, BMNH, MONZ, NZAC, OMNZ).

Distribution. NN, MB, BR, NC: mountain ranges — Boulder Lake, Tasman Mtns (Domett Ra., Aorere Peak), Lockett Ra., Mt Cobb, Peel Ra., Arthur Ra., Owen Ra., Marino Mtns, Richmond Ra., Black Birch Ra., St Arnaud Ra., Travers Ra., Victoria Ra., Lewis Pass, Hanmer Ra. (Mt Miromiro), Polar Range (Mt Dome), Arthurs Pass, Broken R. Basin.

Host plants. Aciphylla monroi, Anisotomesp. (Apiaceae).

Remarks. Lyperobius fallax is illustrated in a colour photograph by Meads (1990: 47).

Lyperobius glacialis new species

Figures 35, 60; Map 13

Type data. Holotype: male, WD, Fox Glacier, Chancellor Shelf, 1340 m, 13 December 1984, J.W. Early, from base of *Aciphylla* sp. (NZAC), 19.4×8.8 mm.

Paratypes: 4 males, same data as holotype, J.W. Early & P. Syrett; 3 females, same data except 1280 m, 15 Dec 1984; 1 female, same data except 1280 m, P. Syrett; 1 female, WD, Westland National Park, Castle Rocks V[ly], 1250 m, 15 Jan 1986, J.W. Early, *Aciphylla*; I female, WD, Fox Glacier, Chancellor Hut, 1220 m, litter LUNZ 84/8, J.W. Early & P. Syrett; I female, WD, Mt Moltke, 5000 ft [1500 m], above Franz Josef Glacier, 20 Jan 1925.

Description. Length 18.2–21.9 mm, width 8.1–10.5 mm. Integument reddish brown to black; body vestiture of elongate-ovate, yellowish-white scales, densest on head, sides of pronotum, and elytral intervals 2, 4, and 6. Rostrum relatively long and thin, 2.2–2.6× its apical width. Funicle with 1st segment 1.6–1.9× as long as 2nd segment. Pronotum transverse, 1.1–1.3× wider than long, with sides strongly rounded and with a shallow median basal impression. Elytra elongate elliptic; intervals 3 and 5 distinctly costate on disc; interval 7 flat to slightly raised, strongly granulate; interval 3 flat on declivity.

Male. Ventrite 5 with a distinct medio-apical impression. Median lobe stout; aedeagal apodemes shorter than median lobe. Endophallus with apical sclerites; basal sclerite without apicolateral processes (Fig. 60).

Female. Ventrite 5 almost flat medio-apically, with lateral impressions. Sternite 8 with apodeme relatively long. Hemisternites with distal portion elongate; hemisternal pouches more than half length of hemisternites.

Material examined. Type series only (AMNZ, LUNZ, NZAC).

Distribution. WD: mountains surrounding Fox Glacier and Franz Josef Glacier (Mt Moltke, Castle Rocks, Chancellor Shelf).

Host plant. Aciphylla sp. (Apiaceae).

Remarks. Lyperobius glacialis is distinguished by the combination of elytral interval 3 flat on declivity, interval 7 barely costate and heavily granulate, endophallus basal sclerite without apicolateral processes, and bursa copulatrix without a sclerite near junction with oviduct.

Lyperobius hudsoni Broun

Figures 6, 17, 21, 25, 37, 61; Map 14

hudsoni Broun, 1914: 127 (Lyperobius). –Hudson 1923:
 390. –Tillyard 1926: pl. 2 fig. 18. –Dalla Torre,
 Schenkling, & Marshall 1932: 65. –Hudson 1934:
 133, pl. XIII fig. 2.

Type data. Lectotype: female (here designated), CO, "Humboldt Range, 5600 ft [1680 m], GV Hudson" (BMNH), 16×7.7 mm.

Redescription. Length 11.5-21.5 mm, width 5.9-9.3 mm. Integument black; body vestiture of white or yellowish, oval to ovate scales, densest on base of head and sides and middle of pronotal disc, and forming distinct pale stripes in elytral intervals 2, 4, and 6. Rostrum relatively long and thin, 2.06-2.6× its apical width (Fig. 17). Funicle with 1st segment twice as long as 2nd segment; segments 3-7 distinctly transverse, except in Humboldt Mountains populations (Fig. 17). Pronotum subsquare, length 0.95-1.07× width, with sides subparallel to gently rounded; disc with pale scale stripes in narrow lateral and median longitudinal sulci (Fig. 21). Elytra elongate oval to elongate ovate; intervals 3, 5, and 7 raised as costae; interval 9 raised as costae on apical quarter; intervals 2, 4, and 6 usually flat, sometimes with transverse raised areas joining costae in intervals 3, 5, and 7 and interrupting the pale stripes. Tarsal segments 1 and 2 with apical sole hairs longer than those on segment 3, and greatly projecting distally (Fig. 37).

Male. Ventrite 5 with a distinct medio-apical impression. Median lobe stout; aedeagal apodemes about as long as median lobe. Endophallus with apical sclerites; basal sclerite with apicolateral processes (Fig. 61).

Female. Ventrite 5 convex on basal half, with a shallow medio-apical impression. Sternite 8 with apodeme long.

Hemisternites with abundant fine setae on apical portion; hemisternal pouches short and broad. Bursa copulatrix with a distinct sclerotised area near junction with oviduct.

Material examined. Lectotype, plus 170 non-type examples (AMNZ, BHPC, BIPB, BMNH, MONZ, NZAC).

Distribution. CO, OL: mountain ranges – Forbes Mtns (Mt Tyndall), Humboldt Mtns, Aílsa Mtns, Mt Cardrona, Minor Peak, Ben Lomond, Cecil Peak, Eyre Mtns, The Remarkables, Hector Mtns, Pisa Ra., Kopuwai / Old Man Ra., Old Woman Ra., Garvie Mtns.

Altitudinal range 1600–1900 m on The Remarkables (Patrick et al. 1992), 1600–1690 m on the Old Man Range (Brumley et al. 1986), and 1750–1860 m on the Eyre Mountains (Mark et al. 1989).

Host plants. Aciphylla dobsonii, A. lecomtei, A. simplex, A. spedenii, Anisotome flexuosa, A. imbricata (Apiaccae).

Remarks. Elytral pattern and sculpture vary greatly in *L. hudsoni*. In some individuals elytral intervals 2, 4, and 6 have transverse raised areas joining the costae on the uneven intervals and interrupting the pale scale stripes. Such individuals predominate in Old Man Range and Garvie Mountains populations, but are rare in Pisa Range and Humboldt Mountains populations. This taxon may be a complex of cryptic species.

Lyperobius huttoni Pascoe

Figures 7, 31, 62-64; Map 15

huttoni Pascoe, 1876: 54 (Lyperobius). –Broun 1880: 445. –Hutton 1904: 203. –Hudson 1923: 390. –Dalla Torre, Schenkling, & Marshall 1932: 65. –Hudson 1934: 133.

Type data. Lectotype: male (here designated), MB, Tarndale ["near the head of the river Wairau, in the Nelson province", Captain F.W. Huttou] (BMNH), 20×9 mm.

Paralectotypes (here designated): 2 males, 4 females, same data as lectotype.

Redescription. Length 18–26.2 mm, width 9.2–11.8 mm. Integument reddish brown to black; body vestiture sparse, of white lineal-lanceolate scales, densest on pronotal sides and forming pale, reduced stripes only on elytral declivity. Rostrum relatively short and thick, 1.48–1.69× apical width in length. Funicle with 1st segment 1.33–1.79× as long as 2nd segment; 7th segment transverse. Pronotum transverse, with sides broadly rounded; disc with a mid-basal impression. Elytra elongate elliptic; intervals flat or slightly convex, never distinctly costate.

Tarsal segments 1 and 2 with sole hairs not much longer than those on segment 3, only slightly projecting distally.

Male. Ventrite 5 with a slight medio-apical impression. Median lobe stout; aedeagal apodemes about as long as median lobe. Endophallus with a pair of narrow apical sclerites; basal sclerite triangular, with short apicolateral processes (Fig. 62–64).

Female. Ventrite 5 slightly convex on basal half, with lateral impressions. Tergite 8 broad. Hemisternites broad, stout; hemisternal pouches almost as long as hemisternites.

Material examined. Type series, plus some 200 nontype examples [approximately one-third of them fragmented] (AMNZ, BHPC, BMNH, CMNZ, LUNZ, MONZ, NZAC, OMNZ).

Distribution. North I.—WN: Wellington, southern coast and coastal hills (Happy Valley, Island Bay to mouth of Karori Stream, Hawkins Hill). South I.—MB, KA, NC, MC, SC: Tarndale, upper Wairau Vly; Black Birch Ra.; Seaward Kaikoura Ra. (Haycock Ra., Mt Fyffe, Kahutara Saddle), Jacks Pass, Hanmer Range; Hanmer Plain; Mt Binser; Craig-ieburn Ra.; Horwell Downs Stn, north of Burkes Pass, Two Thumb Ra.; Albury Ra.; Grampian Mtns; Hunters Hills.

The distribution and biogeographic history of this species were discussed and mapped by Craw (1988).

Host plants. Aciphylla aurea, A. colensoi, A. squarrosa (Apiaceae).

Remarks. A threatened and legally protected species, *Lyperobius huttoni* is easily recognised by its non-costate elytral intervals, sparse body vestiture, and short, thick rostrum. South Island populations, found in montane to subalpine habitats, have an eastern distribution from the Black Birch Range (Marlborough) to the Hunters Hills (South Canterbury).

North Island populations were discovered on coastal cliffs and hills south of Wellington by A.C. O'Connor and A.E. Brookes in 1917. These populations once extended from Island Bay to the mouth of the Karori Stream, but by the late 1980s *L. huttoni* was facing extinction in these coastal habitats. A fenced reserve has been established on the south Wellington coast to protect important habitat for this species (Sherley 1994). Ecology and morphology of Wellington coastal populations have been studied in detail (Bull 1967). Hunt (1996) provides further information on the ecology and conservation status of this species.

Lyperobius montanus new species

Figures 8, 28, 34, 65; Map 16

Type data. Holotype: male, FD, Gertrude Saddle, 1350 m, 3 January 1981, B. Patrick (NZAC), 18.3×8.1 mm.

Paratypes: 1 male, FD, Homer Tunnel, 100 m, 5 Dec 1987, B.H. Patrick; 1 male, 6 females, FD, Fiordland N.P., Gertrude Vly, 1150–1380 m, 6 Feb 1980, J.W. Early, R. M. Emberson, & P.T. Townsend; 4 males, 5 females, FD, Gertrude Saddle, Homer, 4500 ft [1350 m], 5 Feb 1963, J.I. Townsend, *Aciphylla congesta & Anisotome haastii*; 1 male, FD, Gertrude Saddle, Homer Tunnel, 4830 ft [1450 m], 5 Feb 1963, R.M. Bull.

Description. Length 13.4–21.8 mm, width 6.3–10.5 mm. Integument black to dark reddish brown; body vestiture of ovate, pale yellowish-white scales, densest on head, sides of pronotum, and intervals 2, 4, and 6, but nowhere as abundant as in most other species. Rostrum relatively long and thin, 2.0–2.3× its apical width. Funicle with 1st seg-ment 1.8–2.2× as long as 2nd segment. Pronotum about as long as wide, with sides gently rounded. Elytra clongate ovate; intervals 3, 5, and 7 weakly raised as low costae; intervals 3 and 9 flat on apical third (Fig. 28); intervals 2, 4, and 6 very slightly raised and transversely rugose. Tarsal segments 1 and 2 with apical sole hairs longer than those of segment 3, and greatly projecting distally.

Male. Ventrite 5 with a distinct medio-apical impression. Median lobe stout; acdeagal apodemes about as long as median lobe. Endophallus with apical sclerites; basal sclerite with short apicolateral processes (Fig. 65).

Female. Ventrite 5 weakly convex on basal half, at most shallowly impressed on apical half. Sternite 8 with apodeme relatively short. Hemisternal pouch short, narrow. Bursa copulatrix with a distinct sclerotised area near junction with oviduct.

Material examined. Type series, plus 88 non-type examples (AMNZ, BHPC, LUNZ, MONZ, NZAC).

Distribution. WD, FD: mountain ranges – Olivine Ra., Red Hill Ra., Darran Mtns, Gertrude Saddle, Homer Saddle, Mackinnon Pass, Murchison Mtns.

Host plants. Aciphylla congesta, Anisotome haastii (Apiaccae).

Remarks. Lyperobius montanus is easily distinguished from all other species by the combination of elytral intervals 3 and 9 flat on apical quarters (Fig. 28) and much less abundant pale scaling on elytra. Colour photographs

of this species can be found in Peat & Patrick (1996) and Morris & Hayden (1995).

Lyperobius nesidiotes Kuschel

Figure 66; Map 17

nesidiotes Kuschel, 1987: 20 (Lyperobius).

Type data. Holotype: male, The Snares, Broughton I., 14 January 1977, D.S. Horning (NZAC), 21.0×10.0 mm. **Paratypes** (*n*=11): listed in Kuschel (1987).

Redescription. Length 20.5–22.5 mm, width 9.3–10.0 mm.

Integument black, with elytra and tarsi often dark reddish brown; body vestiture of orbicular to ovate, greyish-white to yellowish-brown scales, densest on elytral intervals 2, 4, and 6, elytral declivity, and upper inner face of coxae. Rostrum relatively long and thin, 2.25–2.42× its apical width. Funicle with 1st segment 1.58–1.76× as long as 2nd segment; segments 3–7 becoming progressively more transverse. Pronotum slightly transverse, 1.1–1.19× wider than long; disc with a median carina or elongate, flat, smooth line often extending length of pronotum, and with a median basal impression. Elytra elongate elliptic; intervals 3, 5, and 7 raised as low costae; interval 3 with costae obsolete to obsolescent on apical third; interval 9 flat on apical quarter; intervals 2, 4, and 6 flat, convex or subcostate.

Male. Ventrite 5 with a very light medio-apical impression. Median lobe robust, elongate; aedeagal apodemes amost as long as median lobe. Endophalius without apical sclerites; basal sclerite without apicolateral processes (Fig. 66).

Female. Ventrite 5 strongly convex basally, with a deep, transverse medio-apical impression and upturned apical margin. Sternite 8 with apodeme relatively long. Hemisternites with stout setae on proximal part; hemisternal pouches short, broad.

Material examined. Type series only (CMNZ, LUNZ, MONZ, NZAC).

Distribution. The Snares (Broughton I. only).

Host plant. Anisotome acutifolia (Apiaceae).

Remarks. The rarest of all *Lyperobius* species, *L. nesidiotes* is confined to a small islet in The Snares, where it is found in a patch of host plant not much larger than a small room (J.W. Early, pers. comm.).

Lyperobius patricki new species

Figures 22, 42, 43, 67, 74, 81; Map 18

Type data. Holotype: male, CO, Kakanui Mountains, Otepopo Spur, 1240 m, 13 December 1989, B.H. Patrick, on Asciphyllas gracilis (NZAC), 21.7×10.3 mm.

Paratypes: 2 males, 1 female, CO, St Mary's Ra., Awakino Ski Field, 1220 m, 18 Feb 1989, A.C. Harris, Aciphylla aurea; 1 female, CO, St Mary's Ra., 19 Feb 1989, B.H. Patrick; 5 females, CO, Little Mt Domet, 1150–1600 m, 21 Mar 1991, B.H. P[atrick], feeding on A[ciphylla] aurea.

Description. Length 22.3–26.5 mm, width 10–12.5 mm. Integument dark reddish brown; body vestiture of yellowish-grey, lineal-ovate to lineal-lanceolate scales (often hairlike), densest on head and clytral intervals 2, 4, and 6. Rostrum relatively short and thick, length 1.7–1.95× apical width. Funicle with 1st segment 1.33–1.6× as long as 2nd segment; segments 3–6 transverse; segment 7 rounded. Pronotum weakly transverse, 1.07–1.19× wider than long, broadly rounded, with an abbreviated median carina (Fig. 22). Elytra elongate elliptic; intervals 3, 5, and 7 raised as costae; intervals 2, 4, and 6 with large granules, these sometimes confluent and forming vestigial to secondary costae.

Male. Third tarsal segment about as long as broad. Ventrite 5 with a deep, circular, medio-apical impression (Fig. 42). Median lobe short, stout; aedeagal apodemes about as long as median lobe. Endophallus without apical sclerites; basal sclerite with apicolateral processes (Fig. 67).

Female. Ventrite 5 with a deep, circular, medio-apical impression and upturned apical margin (Fig. 43). Sternite 8 stout; apodeme short and thick (Fig. 74). Hemisternites with stout setae on proximal portion; hemisternal pouches short, broad. Bursa copulatrix with accessory lobes (Fig. 81).

Material examined. Type series, plus 16 non-type examples (BHPC, BIPB, NZAC, OMNZ).

Distribution. SC/MK, CO, DN: mountain ranges — Grampian Ra., St Mary's Ra., Little Mt Domet, Ida Ra., Kakanui Ra., Pig Root Creek.

Host plants. Aciphylla aurea, A. montana var. gracilis (Apiaceae).

Remarks. First collected in 1964, Lyperobius patricki occurs as low as 800 m in North Otago and South Canterbury ranges. This large species is distinguished from its vicariant relative L. spedenii by its larger and more

elongate habitus, lineal-ovate to lineal-lanceolate hairlike scales, and non-transverse third tarsal segment (in male), and from its only known sympatric congener *L. barbarae* by size, pronotal sculpture and pattern, and secondary scale stripes in even clytral intervals. A colour photograph of this species can be found in Patrick (1991, fig. 9).

Named for entomologist Brian Patrick, who has contributed new distribution and host plant records plus numerous specimens towards this revision.

Lyperobius spedenii Broun

Figures 9, 23, 68, 75, 82; Map 19

spedenii Broun, 1917: 443 (Lyperobius). –Hudson 1923: 390, –Dalla Torre, Schenkling, & Marshail 1932: 65. –Hudson 1934: 214.

Type data. Holotype: female, SL, "Garvie Mts., nr. Blue Lake, J. Speden, 7.1.1914" (BMNH), 25.2×12.1 mm.

Redescription. Length 17.7–23.8 mm, width 9.1–11.3 mm.

Integument black; body vestiture of orbicular to ovate, pale yellowish-white to grey yellowish-white scales, densest on head and even elytral intervals. Rostrum variable in length, 1.76–2.5× its apical width. Funicle with 1st segment 1.5–1.6× as long as 2nd segment; segments 3–6 transverse; segment 7 variably transverse to about as long as wide. Pronotum transverse, 1.1–1.24× wider than long, with sides gently rounded and then subparallel to sinuate; disc with pale scales scattered in no particular pattern, an elongate, low, flat, smooth median strip, and a distinct median basal impression (Fig. 23). Elytra broadly ovate; intervals 3, 5, and 7 costate; even intervals with large granules, these sometimes confluent and forming secondary to vestigial costae; secondary scale stripes also present.

Male. Third tarsal segment transverse. Ventrite 5 with a medio-apical, obconical to semicircular impression. Median lobe very stout; aedeagal apodemes about as long as median lobe. Endophallus without apical sclerite(s); basal sclerite with apicolateral processes (Fig. 68).

Female. Sternite 8 elongate; apodeme relatively long and thin (Fig. 75). Hemisternites with stout setae on apical portions; hemisternal pouches short. Bursa copulatrix with accessory lobes (Fig. 82).

Material examined. Holotype, plus 36 non-type examples (BHPC, BIPB, BMNH, NZAC).

Distribution. MC, MK, WD, CO, OL, SL: mountain ranges – Mt Hutt Ra., Godley Glacier, Young Ra. (Mt Brewster), Mark Ra., ranges around L. Ohau, Forbes Mtns (Headlong Peak), upper Dart R., Harris Mtns (End Peak,

Niger Peak), The Remarkables, Eyre Mtns, Snowdon Peak, Garvie Mtns, Takitimu Mtns.

Altitudinal range 1700–1800 m on The Remarkables (Patrick *et al.* 1992), 1400–1860 m on the Eyre Mountains (Mark *et al.* 1989), and 1250–1420 m on the Takitimu Mountains (B. Patrick, pers. comm.).

Host plants. Aciphylla lecomtei, A. pinnatifida, A. spedenii, A. simplex (Apiaceae).

Remarks. Lyperobius spedenii is the most widely distributed of the southern species. A colour photograph appears in Peat (1991).

Lyperobius townsendi new species

Figures 10, 24, 69, 76, 83; Map 20

Type data. Holotype: female, SL, Takitimu Mountains, 4000 ft [1200 m], 12 February 1963, *Anisotome*, J.I. Townsend (NZAC), 18.6×8 mm.

Paratypes: 3 males, same data as holotype; 1 male, SL, Takitimu [Mtns], 1500 m, 24 Jan 1981, B.H. Patrick; 2 males, 2 females, type locality, 4300 ft [1290 m], 30 Nov 1962, J.I. Townsend & A.C. Eyles, *Anisotome*; 2 males, 2 females, type locality, 5000 ft [1500 m], 12 Feb 1963, R.M. Bfulll.

Description. Length 13.6–19.8, width 6.1–8.4 mm.

Integument black or dark reddish brown; body vestiture of oval to ovate white scales, densest on sides, middle of pronotal disc, and elytral intervals 2, 4, and 6. Rostrum relatively long and thin, 2.21–2.58× its apical width. Funicle with 1st segment 1.8–2.0× as long as 2nd segment. Pronotum 0.94–1.08× as long as wide, with sides gently rounded; disc with 3 longitudinal scale stripes lying in distinct shallow sulci (Fig. 24). Elytra elongate elliptic; intervals 3, 5, and 7 raised as distinct costae; interval 9 raised as a distinct costa on apical quarter and conjoint with interval 3 on declivity; intervals 2, 4, and 6 flat, never with raised transverse areas. Tarsal segments 1 and 2 with sole hairs longer than those on segment 3, and greatly projecting distally.

Male. Ventrite 5 with a distinct medio-apical impression, Median lobe elongate; aedeagal apodemes longer than median lobe. Endophallus with apical sclerites; basal sclerite with short apical processes (Fig. 69).

Female. Ventrite 5 with a shallow medio-apical impression. Sternite 8 elongate, with apodeme long (Fig. 76). Hemisternal pouch short and broad. Bursa copulatrix with a distinct sclerotised area near junction with oviduct (Fig. 83).

Material examined. Type series only (BHPC, NZAC).

Distribution. SL: Takitimu Mtns (Family Peak, Mt Brown, Spence Peak).

Host plants. Anisotome haastii, A. pilifera (Apiaceae).

Remarks. The elegant and elongate habitus (Fig. 10) and the genitalia of *L. townsendi* serve to distinguish this distinctive species immediately from all others in the genus.

Named for Mr J.I. Townsend, who collected many of the specimens upon which this revision is based.

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APPENDIX 1 Offshore Molytini and related taxa examined in relation to phylogenetic analysis

	.,
Aclees gyllenhali Pascoe	Philippine Islands
A. hirayami (Kono)	East Asia
Aclees sp.	Vanuatu
Anisorrhynchus barbaratus Rossi	Europe
A. monachus Germar	Europe
Apterylobius basalis (Heller)	Borneo, Mt Kinabalu
A. cinctus Marshall	Borneo, Mt Kinabalu
Arniticus gladiator Pascoe	Brazil
A. hylobiodes (Bohcman)	Paraguay
Byzes diversus (Pascoe)	Brazil
B. grammicus (Pascoe)	Peru
B. indutus (Pascoe)	[no locality]
B. nodifer (Boheman)	Brazil
B. retusus (Boheman)	Brazil
B. schmidili (Boheman)	Brazil
B. talpa (Pascoe)	Venezuela
Calvertius tuberosus (Fairmaire	
& Germain)	Chile
Centor porosus Schoenherr	Brazil
Dyscerus elongatus (Roclofs)	Japan
D. laeviventris (Hustache)	Japan
D. orientalis (Motschulsky)	Japan
D. perforatus (Roelofs)	Japan
Epistrophus tumidus Kirsch	Columbia
Eudociminus mannerheimii	
(Boheman)	N. America
Euthycus japonicus Heller	Japan
E. pendleburyi Marshall	Malay Peninsula
Heilipodus brevicornis (Hustache)	
H. choicus (Germar)	Argentina
H. deletangi (Hustache)	Argentina
H. erythropus (Klug)	[no locality]
H. intricatus (Boheman)	Argentina
H. onychinus (Germar)	Paraguay
Heilipus lactarius Germar	Paraguay
Hesychobius nebulosus Marshall	Western Samoa
Hesychobius sp.	Vanuatu
H. vossi Chujo	Japan
Hylobitelus gebleri (Boheman)	Japan
H. haroldi (Faust)	Japan
H. montanus (Kono)	Japan
Hylobius abietis (Linnaeus)	Europe
H. congener (Dalla Torre,	•
Schenkling & Marshall)	N. America
H. pales (Herbst)	N. America
-	Colombia
I. petulans Faust	Colombia
I. plinthoides Kirsch	Ecuador
Liparus baldensis Reitter	Europe
L. coronatus Goeze	Еигоре
	•

L. dirus Herbst	Europe
L. germanus (Linnaeus)	Europe
L. glabiorostris Kuster	Europe
L. seriatopunctatus Heyd.	Turkestan
L. tenebrionoides Pallas	Europe
Marshallius bondari Rosado-Neto	Brazil
M. picturatus (Germar)	Brazil
Metahylobius rubiginosus	
Morimoto	Japan
Orthorhinus aethiops Boisduval	Australia
O, cruciatus Montrouzier	New Caledonia
O. cylindrirostris (Fabricius)	Australia
O. granosparsus Fairmaire	Fiji
O. klugi Boheman	Tasmania
Pachylobius picivorus (Germar)	N. America
Pagiophloeus orientalis	
(Motschulsky)	Formosa
Paramecops farinosa Wiedman	India
P. stapeliae (Marshall)	S. Africa
Pissodes piceae Illiger	Europe
Plethes albolineata Pascoe	Colombia
P. alternans (Guérin)	Colombia
P. scabrosus (Pascoe)	Colombia
P. unguiculatus (Boheman)	Colombia
P. verrucosus Pascoc	Colombia
Porohylobius feae Faust	Burma
Rhecus spursus Champion	Guatemala
Syphorbus turgidus Pascoe	French Guiana

KEY TO GENERA AND SPECIES OF MOLYTINI KNOWN FROM NEW ZEALAND

- 1 Prothorax and elytra with tubercles and knobs (Fig. 1–4); ocular lobes well developed and partly covering eyes; metasternum in front of hind coxac with a distinct projecting tooth (Fig. 29) ... *Hadramphus* .. 2
- —Prothorax and elytra without tubercles and knobs (Fig. 5-10); ocular lobes weakly developed and not partly covering eyes; metasternum in front of hind coxae without a distinct projecting tooth but often with a slight to prominent overhang (Fig. 30, 31)

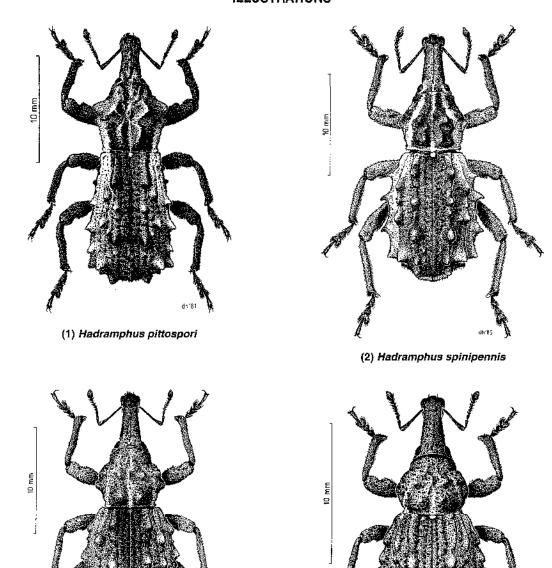
... Lyperobius .. 5

- 2(1) Elytra (in dorsal view) straight sided, widest at apex; 2nd segment of funicle about as long as 1st segment ... (p. 21) .. *H. pittospori*
- —Elytra (in dorsal view) rounded on sides, widest near middle; 2nd segment of funicle distinctly shorter than 1st segment

- 3(2) Elytra with no tubercle on interval 3 in declivity, and no tubercle on interval 9 opposite articulation of ventrites 4 and 5 ... (p. 22) .. H. tuberculatus
- —Elytra with a tubercle on interval 3 in declivity and a tubercle on interval 9, just above articulation of ventrites 4 and 5 ... 4
- 4(3) Elytral interval 7 with spinose tubercles; pronotum with irregular flattened granules; elytra without granules ... (p. 21) .. H. spinipennis
- —Elytral interval 7 with conical tubercles; pronotum and elytra with conspicuous shiny raised granules
 - ... (p. 22) .. H. stilbocarpae
- 5(1) Elytra without any intervals raised as distinct costae (Fig. 7) ... (p. 29) .. L. huttoni
- —Elytra with at least intervals 3 and 5 raised as distinct costae (e.g., Fig. 5, 6, 8, 9) ... 6
- 6(5) Coxae with a distinct dense patch of slightly raised scales on upper half of inner face (Fig. 33) ... 7
- —Coxae without a distinct dense patch of slightly raised scales on upper half of inner face (Fig. 34) ... 9
- 7(6) Elytral intervals 3 and 9 (on declivity) flat or very slightly raised ... (p. 30) .. L. nesidiotes
- —Elytral intervals 3 and 9 (on declivity) raised as distinct conjoint costae ... 8
- 8(7) Pronotum with sides broadly rounded; elytra elongate elliptic, with even and uneven intervals raised as costae ... (p. 23) .. L. australis
- —Pronotum with sides subparallel; elytra broadly elongate ovate, with only uneven intervals on disc raised as costae ... (p. 26) .. L. coxalis
- 9(6) Elytral declivity and apex with all intervals almost flat to slightly convex (Fig. 28) ... 10
- —Elytral declivity and apex with at least intervals 3 and 5, and often 9 as well, distinctly costate (Fig. 27) ... 11
- 10(9) Elytral interval 7 granulate... (p. 28) .. L. glacialis
 —Elytral interval 7 smooth ... (p. 30) .. L. montanus
- 11(9) Elytral disc with secondary scale stripes between striae and costae; main scale stripe composed of scattered pale scales (Fig.26) ... 12
- —Elytral disc without secondary scale stripes between striae and the costae; main scale stripes composed of densely packed pale scales (Fig. 25) ... 17
- 12(11) Even elytral intervals with transverse raised areas ... (p. 27) .. L. eylesi
- —Even elytral intervals with rows of large granules that sometimes are coalesced to form vestigial to secondary costae, especially on basal half of disc ... 13

- 13(12) Pronotal disc with raised areas (if present) largely confined to a median carina or low, flat, narrow elevation that may be abbreviated, and with pale scales scattered in no particular pattern; pronotal sides (in dorsal view) subparallel to sinuate (Fig. 22, 23) 14
 - —Pronotal disc with a distinct, basal to medio-apical, broadly triangular area of low, raised, sparsely punctate elevations that may be separated by longitudinal sulci on either side of a median carina, and with pale scales forming diffuse to distinct, broad lateral stripes; pronotal sides (in dorsal view) narrowly to broadly rounded (e.g., Fig. 20)
 … 15
- 14(13) Elytra elongate elliptic, with disc scales elongate ovate to linear lanceolate; male 3rd tarsal segment almost as long as broad ... (p. 31) .. L. patricki
- —Elytra elongate ovate, with disc scales oval to ovate; male 3rd tarsal segment (in dorsal view) much broader than long ... (p. 31) .. L. spedenii
- 15(14) Elytra elongate ovate; rostrum relatively long and thin (Fig. 16); hind tibiae distinctly sinuate; small species, 14–19 mm in length ... (p. 27) .. L. fallax
 - —Blytra elongate elliptic; rostrum short and thick (Fig. 14); hind tibiac not distinctly sinuate; large species, 20–28 mm in length ... 16
- 16(15) Ventrite 5 in male with a distinct medio-apical impression, in female with basal half distinctly convex (in lateral view) ... (p. 24) .. L. carinatus
- —Ventrite 5 in male with an indistinct medio-apical impression (Fig. 40), in female with basal half plane (in lateral view) ... (p. 25) .. L. clarkei
- 17(11) Rostrum short and thick (length 1.6–1.7× width) (Fig. 15); elytra oval; pronotum much wider than long (Fig. 19) ... (p. 26) .. *L. cupiendus*
- —Rostrum moderately elongate and narrow (length greater than 2x width) (Fig. 17); elytra elongate ovate to elongate elliptic; pronotum about as long as wide or slightly longer than wide ... 18
- 18(17) Elytra elongate elliptic; pronotal disc with lateral sulci interrupted by raised areas just before apical constriction (Fig. 24) ... (p. 32) .. L. townsendi
- Elytra elongate ovate; pronotal disc with lateral sulci and pale scale stripes not interrupted by raised areas just before apical constriction (Fig. 18, 21)
 ... 19
- 19(18) Pronotal disc with lateral and median sulci diffuse and indistinct, sometimes obsolete or obsolescent (Fig. 18) ... (p. 24) .. In barbarae
- —Pronotal disc with lateral and median sulci narrow and distinct (Fig. 21) ... (p. 28) .. L. hudsoni

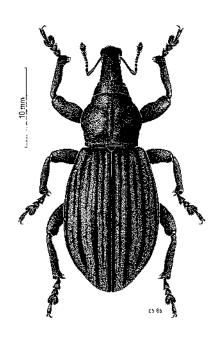
ILLUSTRATIONS



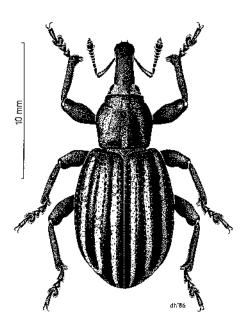
(3) Hadramphus stilbocarpae

(4) Hadramphus tuberculatus

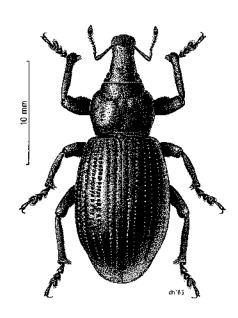
Fig. 1–10 Habitus illustrations of representative Molytini (illustrator: D.W. Helmore).



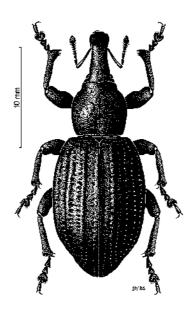
(5) Lyperobius clarkei



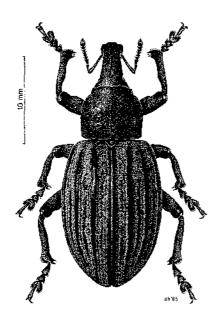
(6) Lyperobius hudsoni



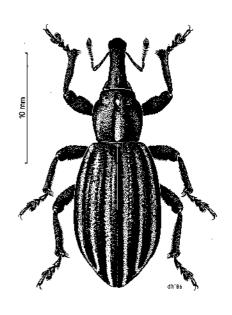
(7) Lyperobius huttoni



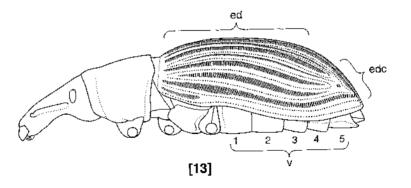
(8) Lyperoblus montanus



(9) Lyperobius spedenii



(10) Lyperobius townsendi



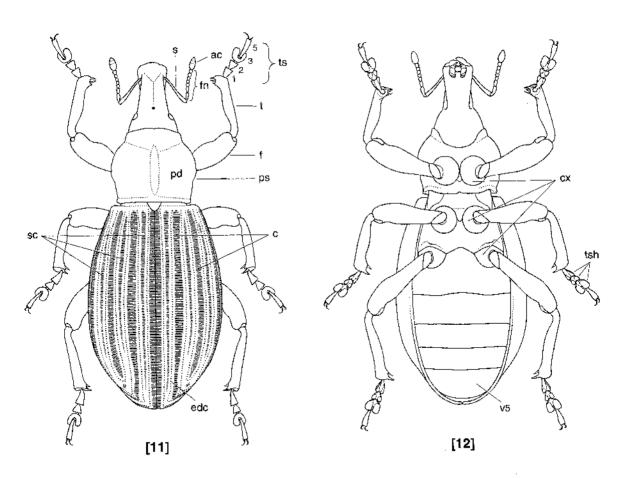


Fig. 11–13 Morphological features used in this study, based on *Lyperobius clarkei*: (11) dorsal; (12) ventral; (13) lateral. Abbreviations: ac - antennal club; c - elytral costae; cx - coxae; ed - elytral disc; edc - elytral declivity; f - femur; fn - antennal funicle; pd - pronotal disc; ps - pronotal side; s - antennal scape; sc - elytral secondary costae; t - tibia; ts - visible tarsal segments; tsh - tarsal sole hairs; v (1, 2, 3, 4, 5) - abdominal ventrites 1–5.

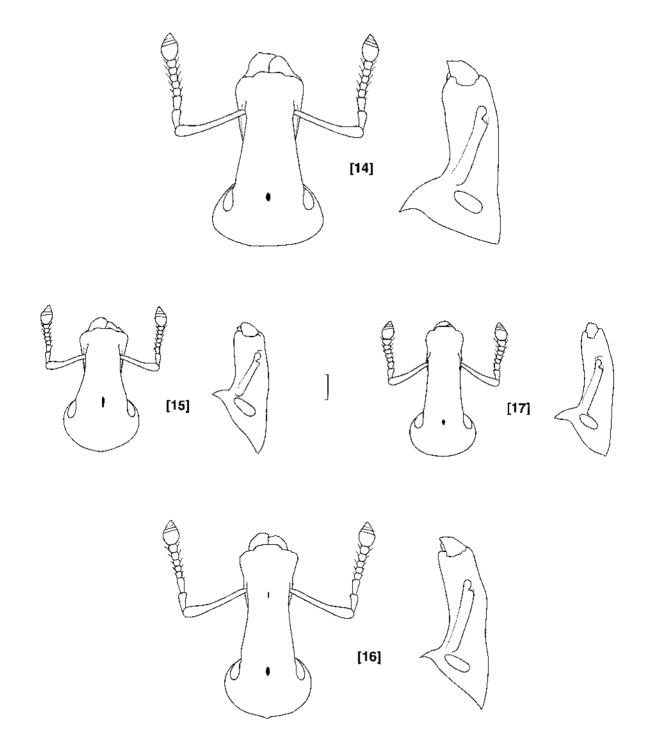


Fig. 14–17 Head, rostrum, and antennae, dorsal and lateral: (14) *Lyperobius clarkei*; (15) *L. cupiendus*; (16) *L. fallax*; (17) *L. hudsoni.* (Fig. 14–83 Scale lines 1.0 mm unless otherwise indicated).

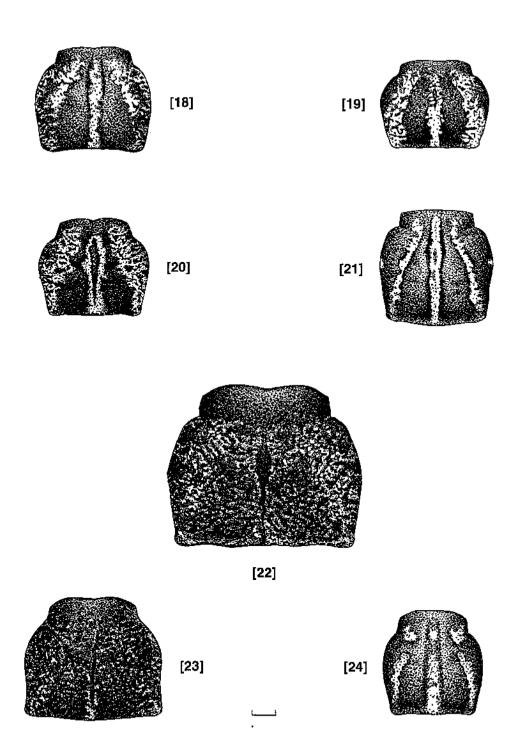


Fig. 18–24 Pronotum: (18) Lyperobius barbarae; (19) L. cupiendus; (20) L. fallax; (21) L. hudsoni; (22) L. patricki; (23) L. spedenii; (24) L. townsendi.

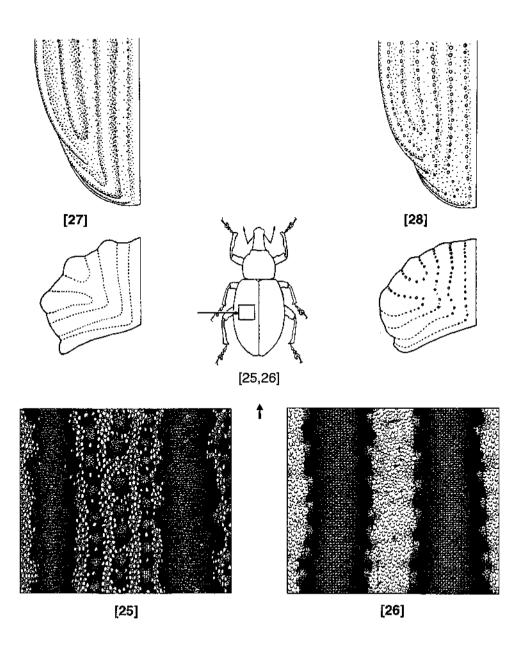


Fig. 25, 26 Scale pattern between intervals 3 and 5 on elytral disc: (25) L spedenii, (26) Lyperobius hudsoni. Fig. 27, 28 Apical half of elytral disc and declivity, in dorsal and rear views: (27) Lyperobius eylesi; (28) L. montanus.

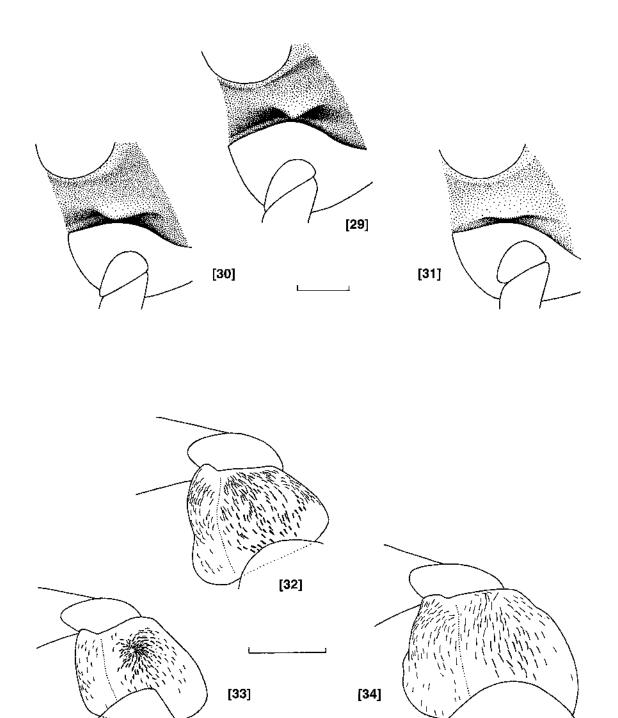


Fig. 32-34 inner face of coxa: (32) Hadramphus stilbocarpae; (33) Lyperobius coxalis; (34) L. montanus.

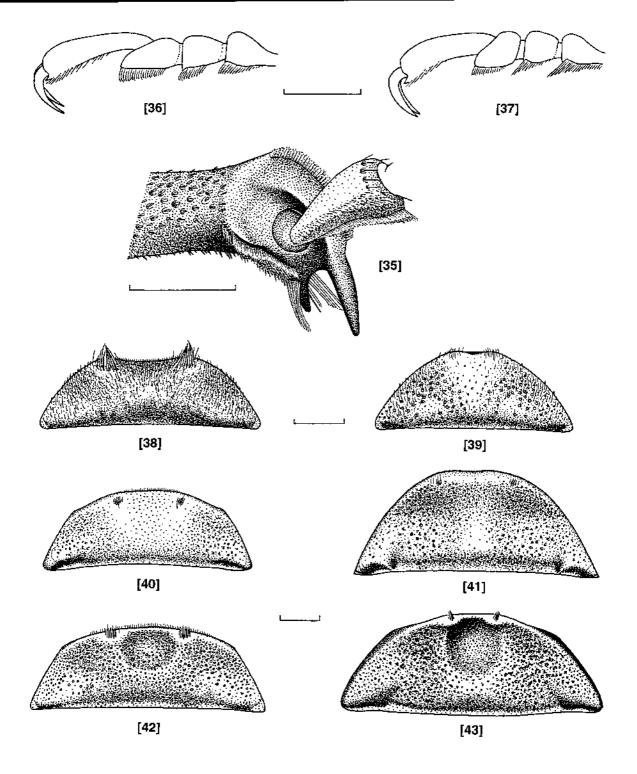


Fig. 35 Apex of tibia, Lyperobius glacialis. Fig. 36, 37 Tarsus, lateral: (36) Lyperobius fallax; (37) L. hudsoni. Fig. 38-43 Fifth ventrite, male and female: (38, 39) Hadramphus stilbocarpae; (40, 41) Lyperobius clarkei; (42, 43) L. patricki.

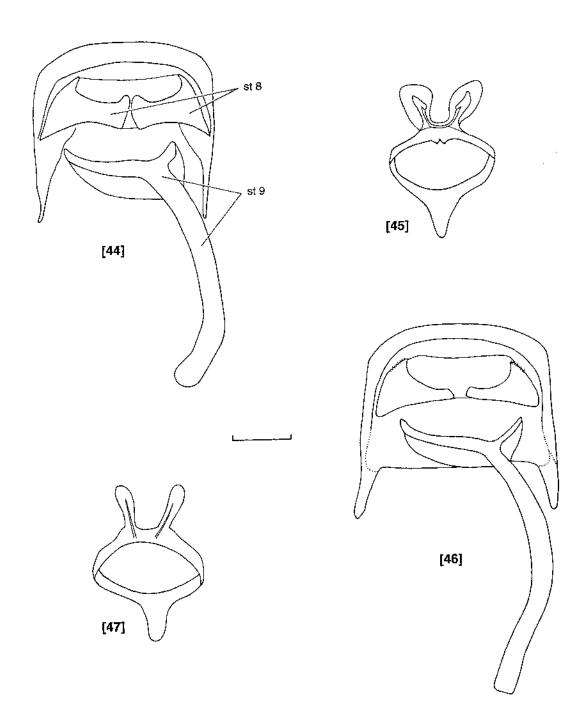


Fig. 44–47 Male 8th abdominal segment plus 9th sternite, ventral, and male tegmen, dorsal: (44, 45) *Hadramphus pittospori*; (46, 47) *H. stilbocarpae*.

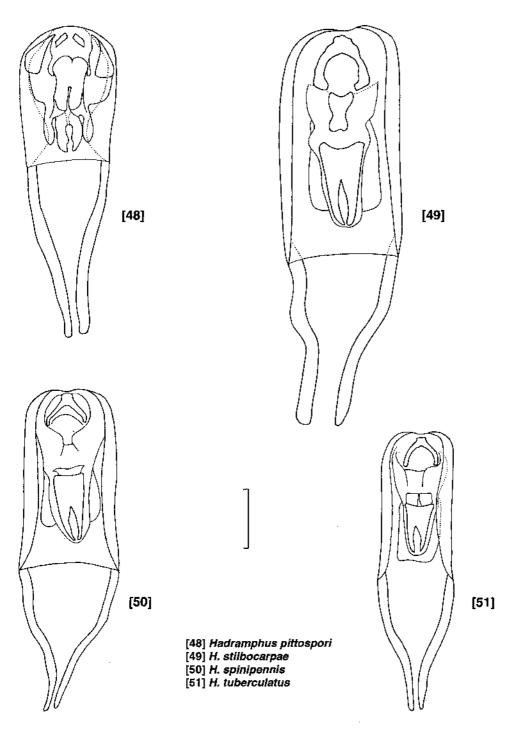
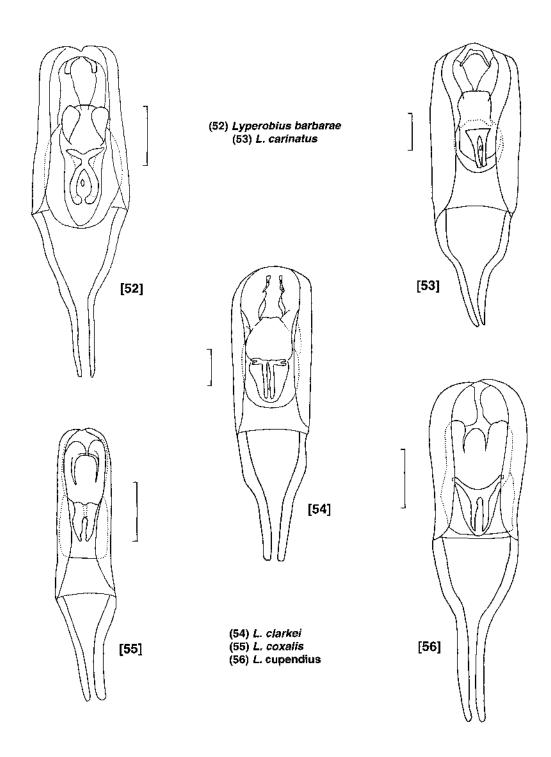
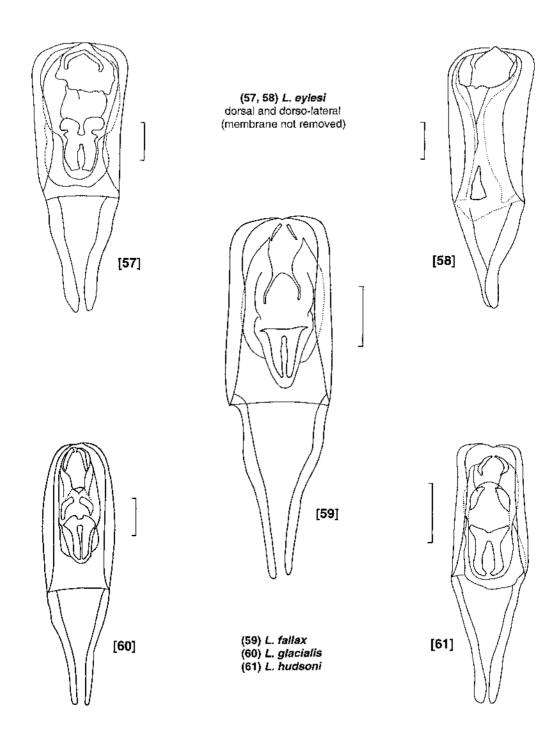
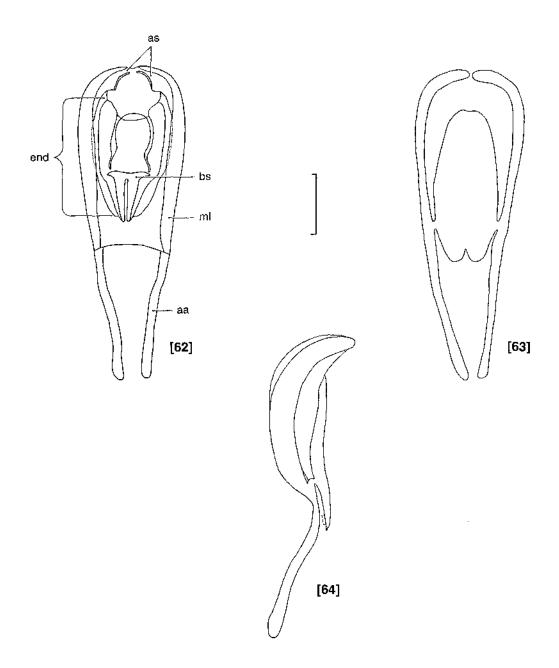


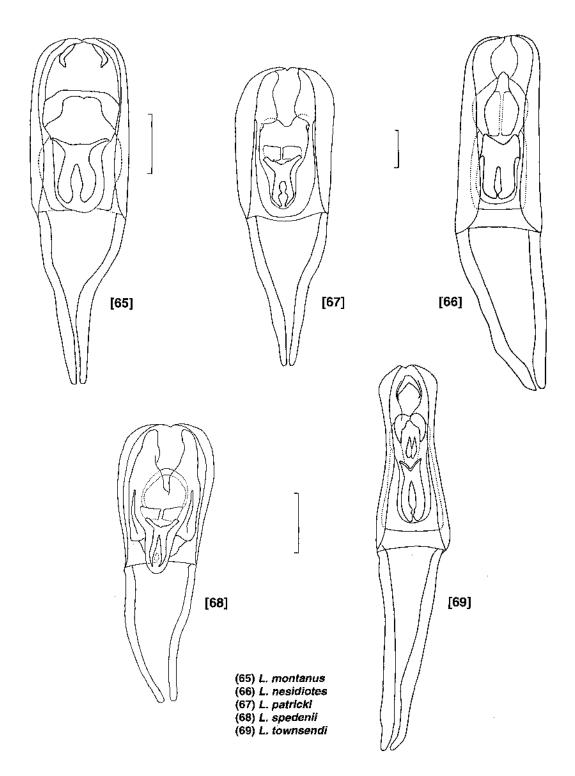
Fig. 48–69 Aedeagus, dorsal unless otherwise indicated (Abbreviations: aa - aedeagal apodemes; as - endophallus apical sclerites; bs - basal sclerite; end - endophallus; ml - median lobe).







(62-64) *L. huttoni* dorsal, ventral, and lateral



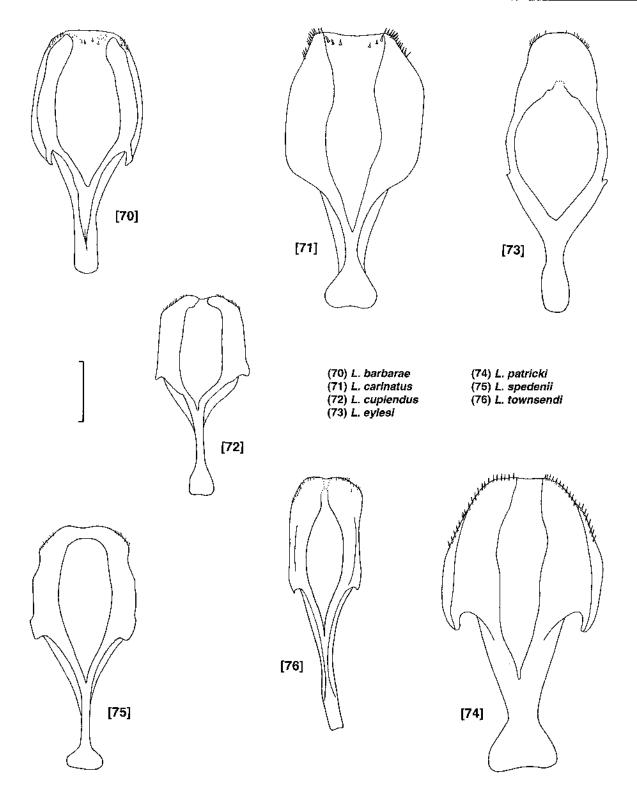
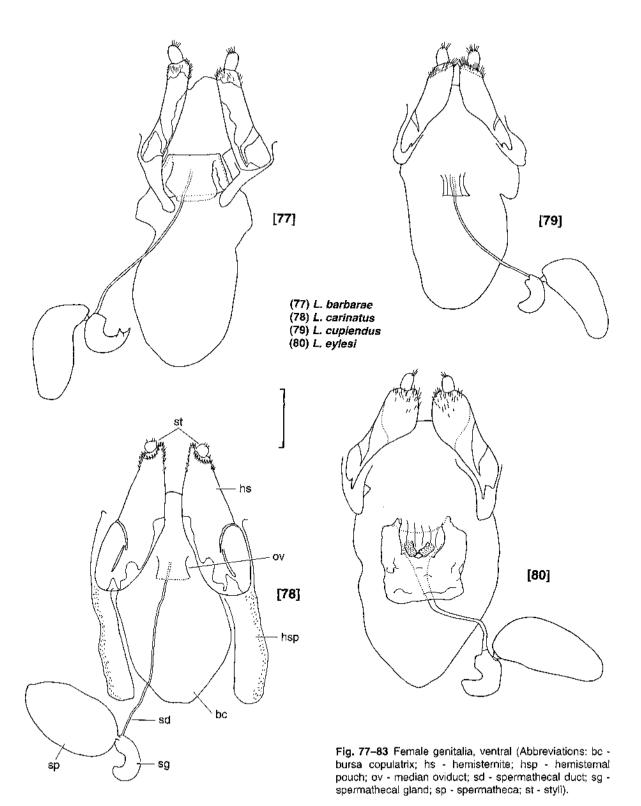
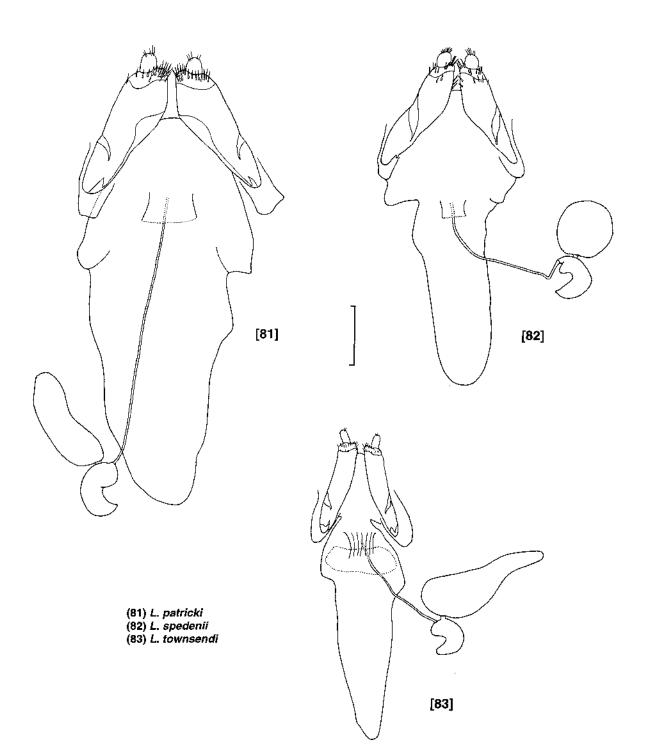
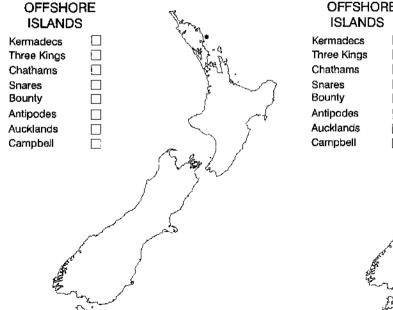


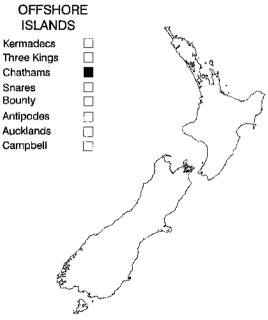
Fig. 70-76 Female 8th sternite, ventral.



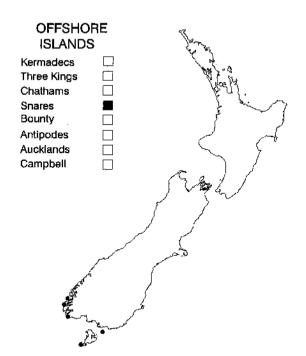




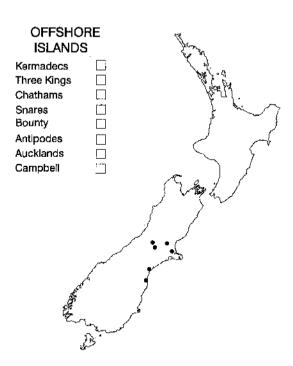
Map 1 Collection localities, Hadramphus pittospori.



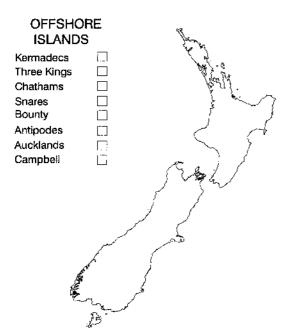
Map 2 Collection localities, Hadramphus spinipennis.



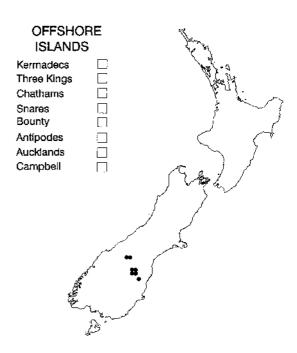
Map 3 Collection localities, Hadramphus stilbocarpae.



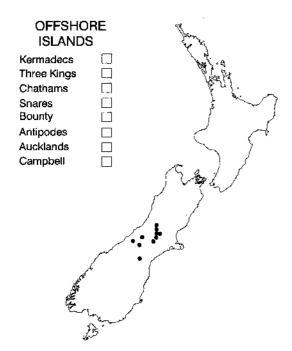
Map 4 Collection localities, Hadramphus tuberculatus.



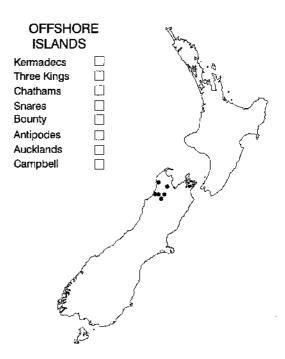
Map 5 Collection localities, Lyperobius australis.



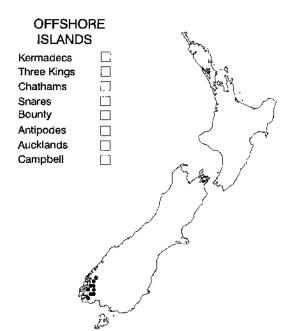
Map 6 Collection localities, Lyperobius barbarae.



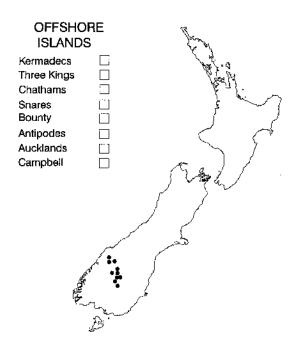
Map 7 Collection localities, Lyperobius carinatus.



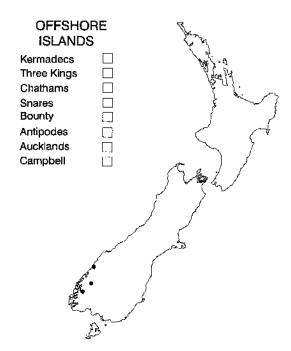
Map 8 Collection localities, Lyperobius clarkei.



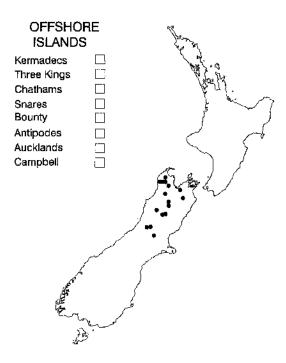
Map 9 Collection localities, Lyperobius coxalis.



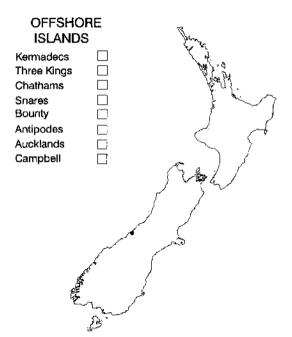
Map 10 Collection localities, Lyperobius cupiendus.



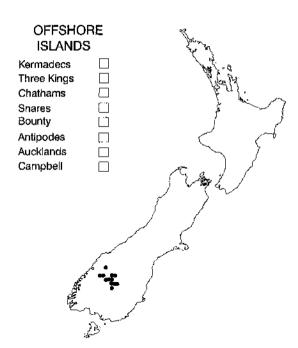
Map 11 Collection localities, Lyperobius eylesi.



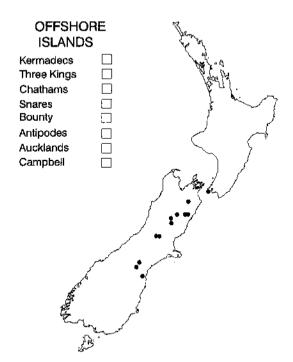
Map 12 Collection localities, Lyperobius fallax.



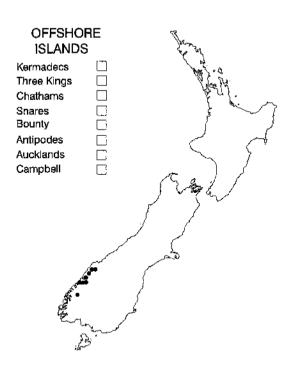
Map 13 Collection localities, Lyperobius glacialis.



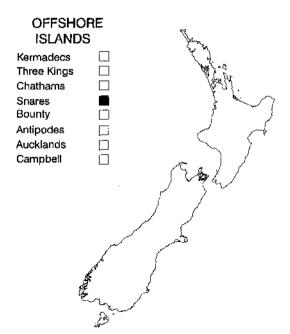
Map 14 Collection localities, Lyperobius hudsoni.



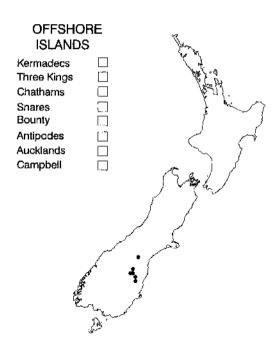
Map 15 Collection localities, Lyperobius huttoni.



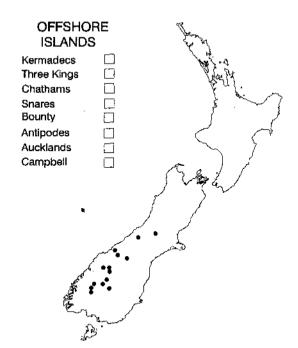
Map 16 Collection localities, Lyperobius montanus.



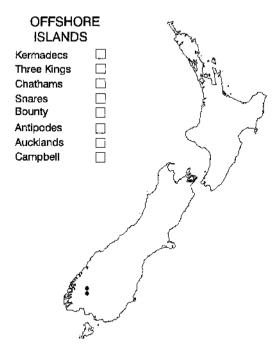
Map 17 Collection localities, Lyperobius nesidiotes.



Map 18 Collection localities, Lyperobius patricki.



Map 19 Collection localities, Lyperobius spedeni.



Map 20 Collection localities, Lyperobius townsendi.

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This index covers the nominal taxa mentioned in the text, regardless of their current status in taxonomy. Page numbers in boldtype denote a description, and in italic type illustrations. A suffixed letter 'k' indicates a key, and 'm' a map.

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Stilbocarpa Iyallii 22

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APPENDIX 2 Host-plant associations of New Zealand Molytini

APIACEAE Aciphylla

aurea : L. huttoni, L. patricki

colensol : L. huttoni

congesta : L. cupiendus, L. eylesi, L. montanus

crosby-smithii ; L. coxalis dieffenbachii ; H. spinipennis dobsonii : L. barbarae, L. hudsoni

ferox : L. clarkei flexuosa: L. barbarae

glaucescens: H. tuberculatus

lecomtei : L. cupiendus, L. hudsoni, L. spedenii

Ivallii: L. coxalis monroi : L. fallax

montana var, gracilis ; L. barbarae, L. patricki pinnatifida: L. coxalis, L. cupiendus, L.

simplex: L. cupiendus, L. hudsoni, L. spedenii

spedenii : L. hudsoni, L. spedenii

squarrosa: L. huttoni

subflabellata: H. tuberculatus

sp. : L. carinatus, L. eylesi, L. glacialis

Anisotome

acutifolia: L. nesidiotes aromatica : L. coxalis

capillifolia : L. coxalis

flexuosa : L. cupiendus, L. hudsoni

haastii : L. coxalis, L. montanus, L. townsendi

imbricata : L. cupiendus, L. hudsoni

Ivallii: H. stilbocarpae pilifera: L. townsendi sp. : L. australis, L. fallax

ARALIACEAE

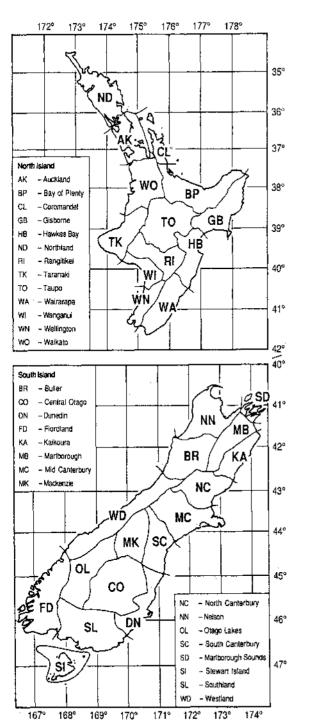
Stilbocarpa

lyallii: H. stilbocarpae robusta: H. stilbocarpae

PITTOSPORACEAE

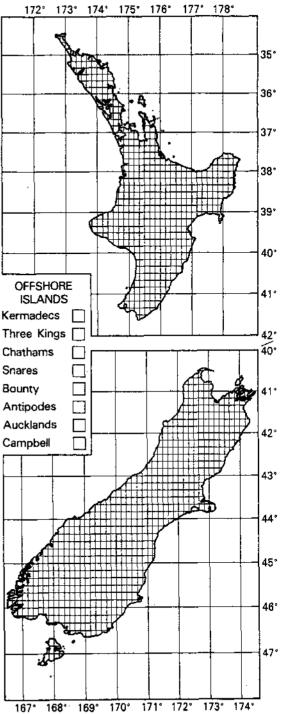
Pittosporum

crassifolium : H. pittospori

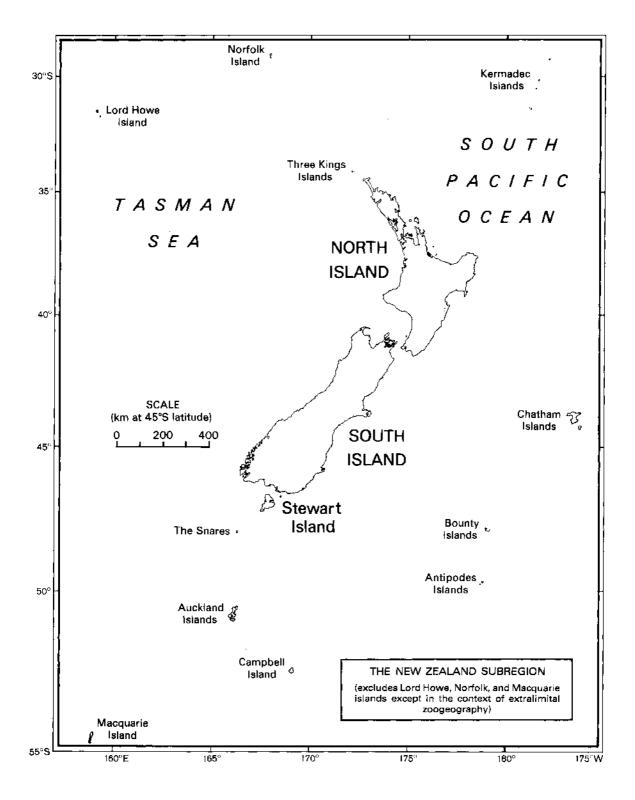


Area codes and boundaries used to categorise specimen locality data (after Crosby et al. 1976)

173°



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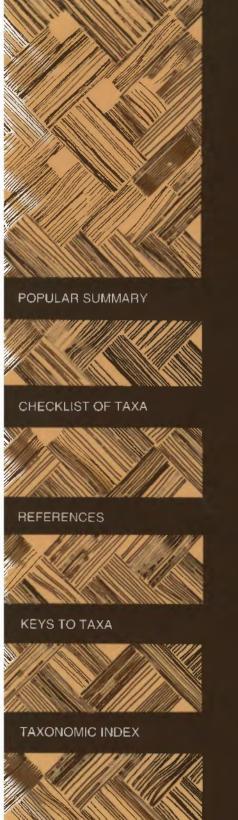
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(Insecta: Coleoptera:

Curculionidae:

Molytinae)

Robin C. Craw



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Craw, R.C. 1999: Molytini (Insecta: Coleoptera: Curculionidae: Molytinae). Fauna of New Zealand 39, 68 pp.

Date of publication: 4 February 1999

Fauna of New Zealand, ISSN 0111-5383; 39 ISBN 0-478-09325-X

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