

**Fauna of  
New Zealand**  
Ko te Aitanga Pepeke  
o Aotearoa

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**Fauna of New Zealand**  
**Ko te Aitanga Pepeke o Aotearoa**

**Number / Nama 42**

# **Aphodiinae**

**(Insecta: Coleoptera: Scarabaeidae)**

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**Manaaki**  
**Whenua**  
**P R E S S**

**Lincoln, Canterbury, New Zealand**  
**2001**

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### **Cataloguing in publication**

STEBNICKA, Z. T. (Zdzisława Teresa), 1932–  
Aphodiinae (Insecta: Coleoptera: Scarabaeidae) / Z. T. Stebnicka  
  
– Lincoln, Canterbury, N.Z. : Manaaki Whenua Press, 2001.  
(Fauna of New Zealand, ISSN 0111–5383 ; no. 42).  
ISBN 0-478-09341-1

I. Title II. Series

UDC 595.764.1(931)

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

Maori text by H. Jacob, Huatau Consultants, Levin.

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

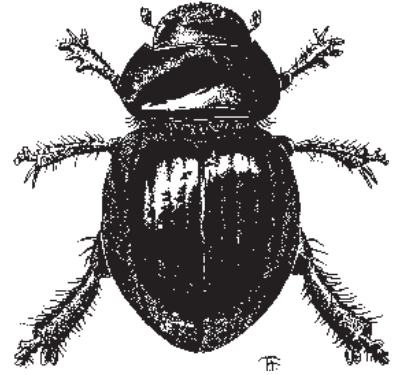
Printed by PrintLink Ltd, Wellington

Front cover: *Acrossidius tasmaniae* (Hope) (Illustrator: D. W. Helmore).

**Publication of the *Fauna of New Zealand* series is the result of a research investment by the Foundation for Research, Science and Technology under contract number C09X002.**

## POPULAR SUMMARY

## HE WHAKARĀPOPOTOTANGA

Class **Insecta**Order **Coleoptera**Family **Scarabaeidae**Subfamily **Aphodiinae**

**Illustration / Whakaahua:** *Phycocus graniceps* Broun (Illustrator / Kaiwhakaahua: A. C. Harris).

**Dung beetles**

Representatives of the Aphodiinae are found throughout the world but it is generally assumed that the warm part of the Old World is their centre of distribution. The New World and Australia, on the other hand, possess only very few members of those tribes and genera that occur in the Old World — instead, endemic genera and species of other tribes of Aphodiinae are numerous.

Approximately 3100 species of aphodiines are known, and many more may be expected, especially from the Neotropical and Oriental regions. The beetles are variously shaped and sculptured, and range from 0.8 mm to 16.0 mm in length. They are most commonly called “dung beetles”, though in fact only a part of this subfamily is usually collected in dung. Aphodiinae are coprophagous or saprophagous, feeding and breeding in the soil on various kinds of excrement and/or in vegetable debris. Several species found in Europe, Asia, America, and Australia, and two species (*Acrossidius tasmaniae* (Hope) and *Ataenius picinus* Harold) in New Zealand have been studied as minor pests of cultivated plants. Some species, e.g., *Phycocus graniceps* Broun and *Tesarius sulcipennis* (Lea), are strongly associated with coastal sand dunes. Many species in other countries are associated with ants and termites and some others live in the burrows of small mammals. A few species are known to be kleptoparasitic, breeding in the brood balls of nest-building dung beetles (Scarabaeidae: Scarabaeinae). Adults of Aphodiinae are attracted to light and are often found in various kinds of excrement, in decaying vegetation, under logs and moss, in rotten wood, and under loose bark of dead trees. The immatures are known for a relatively small number of species.

(continued overleaf)

**Ng~pSara tāae**

Kitea ai ng~mea o te wh~nau iti Aphodiinae i ng~koko katoa o te ao, heoi ko te whakapae, ko ng~w~hi mahana o te ‘Ao Tawhito’ tC~rou tino k~inga. O ng~iwi me ng~puninga ka kitea i reira, he ruarua noa iho ka kitea anC~ te ‘Ao Hou’ me Ahitereiria. Heoi, ko te nuinga o ng~puninga me ng~iwi ka kitea i ‘nei takiw~, k~ore e kitea i w~hi k’.

Kei te ~hua 3100 ng~momo aphodiine e mC~iotia ana, otir~, ar~ noa atu pea ng~momo k~ore anC~i ~ta tautuhia. E tino h~ngai ana t’nei whakapae ki ng~takiw~ o te Pāo Amerika me Amerika ki te Tonga, tae atu ki }hia. He rerek’ te hanga o t’n~, o t’n~ ~, ko te rahi, kei waenga i te 0.8 mm me te 16.0 mm. Ko te ‘pSara tāae’ tC~rou ingoa k~rangaranga, engari ko t’tahi w~hanga noa iho o t’nei wh~nau iti ka kitea e noho ana i te tāae. He kai tāae, he kai popo ng~aphodiinae, ~, ka kitea e kai ana, e whakaputa uri ana i roto i ‘nei mea i te oneone. Kua rangahaua ng~momo maha tonu e noho ana i āropi, i }hia, i Amerika, me Ahitereiria, me ‘tahi momo e rua o Aotearoa (ko te *Acrossidius tasmaniae* (Hope) me te *Ataenius picinus* Harold), he kaikai m~ra nC~rou. Ar~ anC~ tahi momo p’r~i a *Phycocus graniceps* Broun me te *Tesarius sulcipennis* (Lea) e kitea nuitia ana ki ng~t~huna o te tahamoana. He maha ng~momo i t~w~hi e noho ana i waenga i a ng~i pC~okorua me ng~i pC~okotea, ko ‘tahi anC~e noho ana ki ng~rua o ‘tahi kararehe wh~ngote moroitia. Ko ‘tahi momo ruarua nei, ka wh~nako i ng~kC~anga o ng~pSara tāae hanga kC~anga (ar~ ng~Scarabaeidae: Scarabaeinae), hei w~hi whakaputa uri mC~r~rou. Whaiwhai ai ng~aphodiinae pakeke i te m~rama. Ka kitea nuitia hoki i ng~momo tāae maha, i ng~popo,

(haere tonu)

Twenty species of Aphodiinae are now known from New Zealand. Eleven of these have been introduced, probably through human commerce — six are from Australia, two from America, one from Africa, and the last two are cosmopolitan species of European derivation.

The remaining nine species of the genera *Phycocus* Broun (introduced to Tasmania) and *Saprosites* Redtenbacher are indigenous to New Zealand. One species is found only on the South Island, and seven are found only on the North Island including one species collected also on the Kermadec Islands, and one on the Chatham Islands. One species is indigenous to the Three Kings Islands, one to the Chatham Islands, and one to the Kermadec Islands (introduced to the North Island). The non-endemic species, of adventive origin are frequently abundant and conspicuous in towns, orchards, pastures, and other modified environments. The faunal relationships of the native New Zealand Aphodiinae are clearly closest to those of Australia.



Contributor **Zdzisława Teresa Stebnicka**, family name Eichler, was born in Poland, educated in fine arts and natural sciences, and was awarded a Dr. Sc. degree at the Polish Academy of Sciences in Cracow. She is employed at the Institute of Systematics and Evolution of Animals of the Polish Academy of Sciences where her research is on the taxonomy, comparative morphology, biogeography, and phylogeny of various groups of beetles, and in particular the Aphodiinae of the world. She has authored over 80 original papers and books covering systematics, faunal, ecological, and biogeographical treatments of aphodiines and many other groups of Coleoptera. [Photograph: Dr Stebnicka at the Canadian Museum of Nature, Ottawa, June 2000; by François Génier].

i raro i ng~poro r~kau me ng~pākohu, i ng~r~kau pirau, i raro r~nei i te hiako o ng~r~kau kua mate noa. E mōtiotia ana te hanga kōhungahunga o ‘tahi momo ~hua ruarua nei.

E rua tekau ng~momo Aphodiinae o Aotearoa e mōtiotia ana in~ianei. Tekau m~tahi o ‘nei, kua rere mai i t~w~hi, n~ng~mahi tauhokohoko pea i heri mai. E ono i tau mai i Ahitereiria, e rua mai i Amerika, kotahi mai i } wherika, e rua atu an~n~āropi taketake ake, engari kua puta atu ki ng~hau e wh~.

T~r~ an~ng~momo e iwa o te puninga *Phycocus* Broun (kua tae atu an~n~ki Tahim~nia) me *Saprosites* Redtenbacher, he momo tāuru n~ā Aotearoa. Kotahi te momo ka kitea i Te Waipounamu anake, e rima ka kitea i Te Ika a M~ui anake, kotahi ka kitea i Te Ika a M~ui me ng~moutere Kermadec, kotahi an~n~ki Te Ika a M~ui me R~kohu. Kotahi te momo n~m~Manawa-t~whi tāuru, kotahi n~r~kohu tāuru, kotahi n~ng~Kermadec tāuru (kua tau mai an~n~ki Te Ika a M~ui). Ko ng~momo ehara n~konei taketake ake, engari kei konei e noho ana, ka kitea nūitia i ng~taone, i ng~m~ra huar~kau, i ng~p~tss me ‘r~atu taiao n~te ringa tangata i raweke. Ko ng~hono i waenga i ng~Aphodiinae o Aotearoa taketake ake, e ~hua rite ana ki ‘r~o Ahitereiria.

I wh~nau mai te kaituhi, a **Zdzisława Teresa Stebnicka** (ko Eichler tana ingoa wh~nau), i Pōāna. Ko ng~mahi toi me ng~pāāiao m~ori ~na kaupapa matua i te whare w~nanga, ~ka whakawhiwhia ia ki tana T~kutatanga Pāāiao i te W~nanga Pāāiao o Pōāna, i Cracow. Kei te Pāāhi Whakarōā Kunenga Kararehe, i raro i te maru o te W~nanga Pāāiao o Pōāna, a ia e mahi ana. Ko t~na kaupapa rangahau, ko te whakarōā te whakatairite hanga rauropi, te koiiora-matawhenua, me te kunenga o ‘tahi rōāpā Sara, otir~, me te aro wh~iti ki ng~tini Aphodiinae, huri i te ao. Neke atu i te 80 ng~k~Gero n~na an~n~ki tuhi e titiro ana ki te pāāha whakarōā te w~hi noho me te ~hua o t~n~, o t~n~momo, te taupuhi kaiao, tae atu ki te koiiora-matawhenua o ng~aphodiine, me ‘tahi atu huinga Coleoptera maha. [Whakaahua: T~kuta Stebnicka i te Whare Taiao o K~nata, Ottawa, Pipiri 2000; n~François Génier.]

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

## ABSTRACT

The Aphodiinae of New Zealand are comprehensively revised for the first time and their relationships are discussed. Twenty species in 4 tribes and 9 genera are recognised. Two new species are described (*Saprosites kingsensis*, *Saprosites watti*), and 2 new synonymies are proposed (*Ataenius macilentus* Blackburn, 1904 = *A. brouni* (Sharp, 1876); *Saprosites candens* (Broun, 1880) = *S. distans* (Sharp, 1876)). Eleven of the 20 species are introduced, 6 of them originating in Australia, 2 in America, and 1 in Africa; the other 2 are cosmopolitan anthropogenic species of European origin. Members of the genus *Saprosites* Redtenbacher are endemic to New Zealand, except for 1 Australian species. The species of *Phycocus* and *Tesarius* are indigenous to both New Zealand and Tasmania. The morphology and diagnostic characters of aphodiines are reviewed and illustrated in detail. A key is given for the tribes, genera, and species known from New Zealand. The biological associations, known seasonality, and geographic distribution of the species are summarised, with maps indicating locality records. The distributions of the indigenous species and their systematic affinities suggest a Gondwanan origin.

Keywords. Coleoptera, Scarabaeidae, Aphodiinae, New Zealand, taxonomy, classification, key, new species, new synonymy, distribution, ecology, biology, dispersal power, species endemism, fauna.

Stebnicka, Z. T. 2001. Aphodiinae (Insecta: Coleoptera: Scarabaeidae). *Fauna of New Zealand* 42, 64 pp.

Received: 18 March 1999. Accepted: 24 January 2001.

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## ACKNOWLEDGMENTS

The Biodiversity & Conservation Group of Manaaki Whenua initiated this study when they contacted the author in 1996 concerning a possible contribution to the *Fauna of New Zealand* on New Zealand Aphodiinae. This request led over the intervening years to the present revision. During the period of this study I have enjoyed the co-operation in arranging loans of specimens, including types, of a succession of individuals at several institutions. I here thank them, and they are listed with their respective institutions in the section on Abbreviations.

In particular I would like to acknowledge the late Tymone Duval, Trevor Crosby, and Richard Leschen of the New Zealand Arthropod Collection and Rowan Emberson and John Marris of the Lincoln University for their unfailing encouragement and co-operation. Grace Hall assisted greatly through association of specimen lo-

calities with their area codes, and in preparation of the maps. Des Helmore prepared many of the habitus illustrations and Birgit Rhode the SEM's. Rowan Emberson reviewed the manuscript.

The present contribution was supported in part by Grant Nr 6 P04C 055 15 received from the Committee of the Scientific Research (KBN) in Poland.

## INTRODUCTION

The Aphodiinae is a large and diverse group of species inhabiting all zoogeographical regions. The fauna of aphodiines is generally well known for most of the world with the exception of Central and South America. These areas are the object of current studies of the author. The faunas of Australia, New Guinea, and neighbouring archipelagos have been recently treated in a series of papers by Stebnicka & Howden (1994, 1995, 1996, 1997) and Stebnicka (1998b). Before the present contribution was undertaken, very little was known of the faunistic composition of Aphodiinae in New Zealand. Early treatments of New Zealand aphodiines from 1846 to 1910 consist of isolated species descriptions by Broun (6 species), Sharp (4 species), White (1 species), and Lea (1 species). The first native New Zealand species to be discovered was *Saprosites exsculptus* (as *Oxyomus exsculptus*) which was collected at "Port Nicholson" (Wellington) and described by White (1846). Other than the listing of the species in a catalogue (Schmidt 1910) and their misleading diagnoses in a monograph by Schmidt (1922), the only subsequent papers dealing with the taxonomy of New Zealand species were the review of the genus *Saprosites* by Richards (1959) and some synonymical notes by Watt (1984). The status of nearly all species of *Saprosites* has been particularly enigmatic, since their types were not readily accessible to researchers as they were in European collections (mostly in BMNH), and specialists on Aphodiinae never saw them.

The present survey is based mostly on a large holding of material in the New Zealand Arthropod Collection, Auckland, and on the collections of various institutions mentioned in the section on Conventions. Approximately 1800 specimens and the type-series of all New Zealand species were examined. Twenty species are now known from New Zealand, nine of which are indigenous. Eleven are definite introductions from other countries; six from Australia — *Acrossidium tasmaniae* (Hope), *Tesarius sulcipennis* (Lea), *Proctophanes sculptus* ((Hope), *P. minor* ((Blackburn), *Ataenius brouni* (Sharp), *Saprosites mendax* (Blackburn); two from the Americas — *Parataenius simulator* (Harold) and *Ataenius picinus*



Harold; one from Africa — *Australaphodius frenchi* (Blackburn); and two cosmopolitan species of ultimate European origin — *Aphodius lividus* (Olivier) and *A. granarius* (Linnaeus). Two species from the remaining nine are here described as new, and the genera *Tesarius* and *Parataenius* are recognised from New Zealand for the first time. In general, the New Zealand fauna of aphodiines is similar to that of Australia but strongly impoverished in the number of genera and species. The biogeographic affinities of the New Zealand Aphodiinae clearly indicate an ancient, Gondwanan origin in common with the Australian fauna.

## SYSTEMATICS

The higher classification of the subfamily Aphodiinae (Lawrence & Newton 1995) has varied considerably over the last 80 years, and is still not completely settled. The basic systematic arrangement for the world species proposed by Schmidt (1922), based on 1137 species known at that time, is that on which new additions have been based. The latest world catalogue (Dellacasa 1988, 1989, 1991, 1996) lists about 3100 species, but additional taxa have been described since. The tribe Aphodiini forms the core of the subfamily, and is based on the huge genus *Aphodius* Illiger, with over 30 associated genera. The genus *Aphodius* is actually split into about 135 subgenera, with a number of additional species that cannot be properly assigned. Consequently, the existing keys for temperate *Aphodius* have become unworkable, and identification of species very difficult. My belief is that the use of species groups permits organisation within large genera (i.e., *Ataenius*: Stebnicka & Howden 1997) without the attendant nomenclatural problems associated with subgeneric names. It is obvious in these circumstances that a compromise must often be made between the practical aims of classification, its phylogenetic basis, and a system of naming.

The higher categories, such as tribes, genera, and species groups are poorly understood and nearly every author has a different arrangement. Part of the problem is due to the tremendous numbers of species, some of which fill the gaps between any arrangement of higher categories so far devised. Examples of confusion in relationships and classification are numerous, resulting from different levels of knowledge of the various species groups by authors studying only limited faunal areas. Recently a trend may be observed of a category inflation. The breaking up of polyphyletic groups does not necessarily lead to a more practical system, if we do not know where the fragments belong. Various tribes of Aphodiinae have at

one time or another been treated as subfamilies, however, they are not separated by a decided gap (if any), and none of the taxa covered here can seriously be elevated to subfamily rank. As in other groups of Scarabaeoidea, there has been considerable parallel evolution within the subfamily, and almost all characters claimed to be diagnostic at tribal or generic level have evolved independently several times. In some cases, groups which are easily separated in the Old World, e.g., Psammodiini–Eupariini–Aphodiini, become almost indistinguishable in South America or Australia. Often seemingly distinct genera in temperate regions break down in the tropics and potentially strong defining characters are diluted and must be qualified. The following characterisation of Aphodiinae on a world basis and diagnostic characters for tribes found in New Zealand clearly indicate that all taxa above species level have to be defined by a mosaic of characters, a “polythetic classification” — no character in isolation being diagnostic for all members.

## MORPHOLOGY

Characterisations of Aphodiinae (Aphodiidae of authors) hitherto given by many authors are far from being exhaustive and concern mainly superficial, often secondary, characters from casual examples of various groups of species. The following, general description is based on all known tribes, of which only four are represented in New Zealand. The principal characters of the subfamily are first listed here in a synoptic form (excluding sexual dimorphism), and then the tribal characters are discussed at greater length.

General characters used in Aphodiinae for identification are illustrated in Fig. 3–6. A number of species have unusual or unique characters which allow them to be identified without needing to use keys and descriptions.

### PRINCIPAL CHARACTERS OF APHODIINAE

**Body.** Shape and sculpture diverse; length 0.8 mm to 16.0 mm from clypeal apex to elytral apex.

**Head.** Clypeus dilated to cover mouthparts or shortened, exposing mouthparts or clypeus of intermediate type.

Antenna short, of 9, rarely 8, antennomeres, club circular, ovoid, or elongate, of 3 antennomeres.

Eye very large, moderate in size, vestigial or absent.

**Mouthparts.** Maxillary endites (galea and lacinia) separate or approximate, consisting of soft, flexible, densely setose lobes; third maxillary palpomere cylindrical, fusiform or triangular, its length varied.

*Either*: scissorial lobes of mandibles sclerotised, dentate, or truncate; labrum partially sclerotised and more or less exposed in front of clypeus, e.g., Aegialiini (indicates “hard saprophagy” as a component of feeding)

*Or*: scissorial lobes of mandibles dorso-ventrally flattened, flexible plate-like; labrum membranous, fully covered by clypeus, e.g., Aphodiini (indicates “soft saprophagy or coprophagy” as a component of feeding).

**Labrum.** Anterior margin evenly rounded, truncate, bilobed or trilobed; inner surface — epipharynx, consists of various elements and sensory organs (Stebnicka 1985, Stebnicka & Howden 1995, 1996). [Labro-epipharyngeal structures are of some use in species separation, e.g., Aphodiini, and especially indicative at a tribal level].

**Pronotum.** Rectangular or subquadrate in shape; basal and lateral edges margined or not, and/or crenate, explanate or sulcate or otherwise modified; disc evenly convex or sulcate, fossulate and/or carinate, or with hump.

**Scutellum.** From very large to minute; shape triangular, pentagonal, semi-oval, or cordate.

**Elytra.** Striate or not; usually with 10 striae and 10 intervals including sutural ones, or number of striae reduced; rarely elytra non-striate, convergent in sculpture like those of Tenebrionidae, e.g., African *Eremazus* Mulsant; epipleura gradually narrowed to apices, abruptly narrowed or absent posteriorly, or widely inflexed, e.g., Neotropical *Euparixia* Brown, *Euparixoides* Hinton, and *Lomanoxia* Martinez, or with edge upturned, e.g., Neotropical *Selviria* Stebnicka (1999a), and Nearctic *Hornietus* (Stebnicka 2000b); humeral umbone strongly or moderately developed (indicates wings present even if reduced), or humeral area flattened and elytra egg-shaped (indicates wings absent), e.g., Aphodiini, Aegialiini, Psammodiini, and Eupariini; in some species-groups elytra with preapical umbone, e.g., Australian *Podotenus* Schmidt.

**Wings.** Fully developed and functional, or non-functional, brachypterous, or absent.

**Prosternum.** Usually with median tubercle, or with triangular or hastate process.

**Mesosternum.** Evenly convex or deplanate and/or carinate, or with variously shaped callosities, e.g., Asian-Australian *Airapus* Stebnicka & Howden, and Neotropical *Auperia* Chevrolat and *Euparixoides* Hinton.

**Metasternum.** Approximately equal to the length of mesosternum (indicates wings present even if reduced), or significantly shorter than mesosternum (frequently wings absent but not always); surface usually with median longitudinal line or furrow, sometimes with pits; posterior plates frequently with metasternal triangle, e.g., Eupariini and Psammodiini.

**Abdomen.** Five or six sternites visible with intersegmental membranes or sternites coalesced; pygidium covered by elytra or partially exposed, e.g., Proctophanini, Odontolochini, and Eupariini.

**Mesocoxae.** Approximate (space between mesocoxae smaller than width of mesofemur), or moderately separate (space between mesocoxae equal to width of mesofemur), or widely separate (space between mesocoxae nearly twice as wide as mesofemur); coxal cavities parallel or oblique, elongate, rarely round, convergent in shape with those of Zopheridae (Tenebrionoidea and many other beetles), e.g., Neotropical tribe Lomanoxiini (Stebnicka 1999b).

**Metacoxae.** Always contiguous; trochanters short, rarely elongate, e.g., *Phycocus* Broun.

**Legs.** Middle and hind legs short (femora not or barely visible from above), or moderate in length (femora extending a little beyond body outline), or long (femora projecting for about 1/3 their length).

Profemur short, enlarged, flattened dorso-ventrally; meso- and metafemur parallel-sided or fusiform, sometimes posterior edge dentate.

Protibia short or moderate in length, usually with terminal spur; outer side with 1-5 teeth or serrate, e.g., Asian *Setylaides* Stebnicka.

Meso- and metatibia cylindrical, or flattened dorso-ventrally or parallel-sided; transverse ridges clearly developed, e.g., Aphodiini, Proctophanini, and some Aegialiini, Psammodiini, and Eupariini, or vestigial, e.g., some Aphodiini, Psammodiini, Aegialiini, and Eupariini, or absent, e.g., Didactyliini, Odontolochini, Eupariini, and Psammodiini, or tibia otherwise sculptured, e.g., Eupariini; apex of meso- and metatibia with two spurs, rarely with one spur; apical spurs of metatibia slender, spatulate, or foliaceous, placed on each side of tarsal insertion, e.g., Aphodiini and Aegialiini, or placed close together below tarsal insertion, e.g., Didactyliini, Odontolochini, Proctophanini, Psammodiini, and Eupariini, or intermediate character state occurs, e.g., some Aphodiini and Eupariini.

**External sexual dimorphic characters.** Strongly developed to invisible or absent.

**Male genitalia.** Phallobase of aedeagus usually with dorsal hump, junction of phallobase and parameres usually membranous, e.g., Aphodiini, or phallobase of aedeagus evenly rounded, phallobase and parameres sometimes coalesced, e.g., Eupariini and Psammodiini; apical portion of internal sac membranous, frequently furnished with sclerites and/or spicules.

**Female genitalia.** Genital plate “stylus” (the divided 10th

tergite) and its chaetotaxy is of some use in species separation. However, the only paper comprehensively dealing with genital plates is that by Stebnicka (1977).

**Variation.** Aphodiinae show considerable individual variation in the proportions and sculpture of the body. Morphological variants include sexual dimorphism, heterogonic or allometric growth, and geographic variation. Some of the differences are apparently partly associated with size and hence could be considered as allometric. Noticeable geographic variation may be expressed either externally, often in the secondary sexual characters, or in the shape of male genitalia. The latter type of variation can make it difficult to determine the status of allopatric populations.

**Larvae (white grubs).** Body C-shaped, with soft cuticle, except for head capsule and mouthparts. Head usually with a single ocellus on either side, rarely ocelli absent; epicranial suture usually distinct; clypeus transverse, labrum trilobed, freely articulated. Antenna with four (sometimes with five) antennomeres, the last reduced in size, the third usually with conical sensory process. Mandibles asymmetrical; maxilla with galea and lacinia distinctly separate, but often close together, stipes with a row of stridulatory teeth, or without teeth. Legs well developed, with four podites, prothoracic pair shorter. Dorsum of thoracic and abdominal segments plicate; openings of respiratory plates of thoracic spiracles facing posteriorly, those of abdominal spiracles facing ventrally or cephaloventrally; last abdominal segment variously shaped, raster with palidium, occasionally palidium indistinct or absent.

**Pupa** of exarate type, the appendages free.

The immatures have been treated by Ritcher (1966).

### Diagnostic characters for tribes found in New Zealand

**Aphodiini:** body glabrous or covered with hairs; clypeus dilated to cover mouthparts; elytron lacking basal bead; abdominal sternites not fused, with intersegmental membranes; pygidium not exposed, covered by elytra, without scabrous area basally (Fig. 4); mesocoxae approximate, space between mesocoxae usually smaller than width of mesofemur; transverse ridges of meso- and metatibia well developed or occasionally vestigial, apical spurs slender, separated, located on each side of tarsal insertion or nearly so (Fig. 6); phallobase of male aedeagus usually with dorsal hump (Fig. 44) or arcuately rounded (Fig. 46); labro-epipharyngeal complex as in Fig. 33–35.

The male genitalia and the epipharyngeal structures of Aphodiini are usually distinctive and often very useful in identification of species.

**Psammodiini:** body glabrous or covered with setae; clypeus dilated to cover mouthparts; pronotum usually unevenly convex with transverse ridges and furrows, or their vestiges, rarely evenly convex; elytron with or without basal bead; abdominal sternites coalesced, rarely fine intersegmental membranes occur; posterior coxal plates frequently with metasternal triangle, pygidium partially exposed or covered by elytra; mesocoxae approximate or slightly separate, space between mesocoxae usually smaller or equal to width of mesofemur; meso- and metatibia short and robust or elongate and slender, transverse ridges vestigial or lacking, rarely distinctly developed, sometimes metatibia furnished with denticles or tubercles; apical spurs spatulate or slender, located close together below tarsal insertion; phallobase of male aedeagus without dorsal hump (Fig. 47, 48); labro-epipharyngeal complex as in Fig 36.

Psammodiini are most closely related to the Eupariini and either the external morphological characters and/or those of the male genitalia of some groups of species in each tribe overlap. The epipharyngeal structures of Psammodiini differ from the general scheme of those in the Eupariini and are usually sufficient for tribal placement. The differences are evident chiefly in the shape and structure of the anterior median process and in the kinds of sensilla.

**Proctophanini:** body usually glabrous; clypeus dilated to cover mouthparts; elytron lacking basal bead; abdominal sternites coalesced without intersegmental membranes; posterior coxal plates with metasternal triangle, pygidium fully or partially exposed, usually with longitudinal carina at middle; mesocoxae approximate or slightly separated, space between mesocoxae smaller than width of mesofemur; transverse ridges of meso- and metatibia distinct, apical spurs slender, placed close together below tarsal articulation; phallobase of male aedeagus without hump (Fig. 49, 50); labro-epipharyngeal complex as in Fig. 37, 38.

The characters of the male genitalia are useful for identification of species; the epipharyngeal structures are similar to those present in Eupariini. Proctophanini is primarily an Australian–African tribe representing a transitional link between the Aphodiini and the Eupariini. The Australian genus *Proctophanes* and African genera *Australaphodius* Balthasar, *Harmogaster* Harold, and *Drepanocanthus* Péringuey share similar character states and are considered to constitute a separate tribe, the Proctophanini (Stebnicka & Howden 1995).

**Eupariini:** body glabrous or covered with setae; clypeus dilated to cover mouthparts; pronotum usually evenly convex or with slight lateral swellings, rarely with median

hump; elytron with basal bead; abdominal sternites coalesced; posterior coxal plates usually with metasternal triangle, pygidium fully or partially exposed with transverse carina and scabrous area basally (Fig. 27); mesocoxae approximate, slightly separate or widely separate, in some species space between mesocoxae twice as wide as mesofemur; meso- and metatibia cylindrical or flattened, transverse ridges distinct, vestigial or lacking, sometimes metatibia with longitudinal carinae or rows of denticles or tubercles; apical spurs usually slender, placed close together below tarsal insertion; phallobase of male aedeagus usually without hump (Fig. 51–59); labro-epipharyngeal complex as in Fig. 39–43.

Very few descriptions of species of Eupariini include the characters of the male genitalia and of the clypeolabrum. These characters have been examined on a world basis by the author for many species belonging to various taxonomic groups. It has been found that the characters of aedeagus, and the epipharyngeal structures of the Eupariini differ in general from those of the Aphodiini but that they are less useful at the species level. In some euparine groups, the shape of the epipharynx is similar to that of the Psammodiini, but the structures of the anterior median process and some kinds of sensilla are usually sufficient to distinguish the representatives of these two tribes.

## BIOLOGY

Aphodiines occur worldwide, and are often common in various areas ranging from lowlands to the alpine zone and from woodlands to deserts. Most of the species live in open forest clearings, pastures, meadows, and steppes or semi-desert terrains, and occasionally in wooded areas. Species from a number of genera belonging to several tribes have adapted to the xeric environments of coastal and inland sand dunes or alkaline mud flats. The biology and ecology of the group is so diverse that few generalisations can be made.

A salient feature of the natural history of Aphodiinae, both larvae and adults, is connected with the soil. The commonly used name “dung beetles”, is somewhat misleading in that only some taxa in this subfamily are at all frequently collected in dung. Although most temperate aphodiids are coprophagous and breed in the dung of herbivorous mammals, a great number of species are saprophagous in the adult stage, feeding on decomposing plant material. In temperate regions only a small number of species scattered through several genera are commonly found breeding in decaying vegetation, though the fauna found in leaf litter in the tropics is much more diverse. The adaptability of aphodiines to a wide range of diets

has led to the invasion of many specialised habitats. Some species of *Aphodius* are kleptoparasitic, breeding in the brood balls of nest-building Scarabaeoidea, some others live in the burrows of small mammals, and in the above-ground nests of birds; many species of *Ataenius* and *Saprosites* are commonly found in decaying vegetation, in rotten wood, and under loose bark. Certain genera of the Australian and Neotropical tribes have many species that are known to be myrmecophiles and termitophiles, living in more or less close harmony with their hosts, for example members of the tribes Corythoderini (Balthasar 1964, Tangelder & Krikken 1982), Stereomerini (Howden & Storey 1992), Lomanoxiini (Stebnicka 1999b), and Eupariini (Woodruff & Cartwright 1967, Wojcik et al. 1977, Stebnicka 1998a, 1999a) have been observed with the termites *Odontotermes* and with the ants *Atta*, *Solenopsis*, and *Acromyrmex*. Many species exploit the colonies only occasionally, functioning as temporary nest commensals; however, no definite evidence is available to determine if they are synechthrans (unwelcome guests), synoeketes (unnoticed or tolerated guests), or symphiles (true guests). Some myrmecophiles fit more than one of the above categories at different times. Some species are dependent on their hosts during part or all their life cycles. The peculiar morphological features of these beetles, such as trichomes, exudatoria, mycangial structures (Stebnicka 1999c), and presence of the exocrine glands, often indicate their connections with social insects. Flightlessness accompanied by shortening or even loss of the wings, and reduction or loss of the eyes are widespread, and in some of the liquid-feeding symphilic beetles, degeneration of the mouthparts, e.g., Corythoderini. The latter morphological regression suggests the presence of trophallaxis — an exchange of liquid food between the beetles and their hosts. The gradually increasing degree of behavioural integration with the host society constitutes the most obvious of the evolutionary pathways.

To sum up, the two main types of food resource used by the Aphodiinae are herbivore and omnivore dung and decaying vegetation. The species can be divided into two groups according to their diet and the form of the mouthparts of the adults: saprophages and coprophages.

**Saprophages** feed upon dead and decaying plant material that includes leaf litter and moss in forest and scrub lands, logs and tree stumps, rotting fruits, nuts, mushrooms, fallen flowers, compost, and occasional accumulations of flood debris and piles of grass cuttings. Saprophages are distributed around the world according to factors such as type of vegetation, its state of decay, amount of free water in the soil, climate, and other conditions. The saprophages have been divided into two groups (Stebnicka 1985; Cambefort 1991; Stebnicka & Howden

1995, 1996). Species adapted for “hard saprophagy”, using hard organic substances, for example dead wood, leaf litter, mushrooms, and spores, and species adapted for “soft saprophagy”, using semiliquid and liquid contents of decaying vegetation, for example, vegetable juices, dissolved albuminous substances, and/or bacterial albumens in decaying humus. The members of the first category, e.g., tribe Aegialiini: Stebnicka 1977, 1981, 1985; and Stebnicka & Howden 1995, have not been found in New Zealand. The second category includes most species of *Saprosites*, *Phycocus*, *Proctophanes*, and *Ataenius*.

**Coprophages** feed upon various fractions of excreta and all are adapted to “soft saprophagy”. They are found in nearly all kinds of dung. Large herbivores eat huge quantities of grass and other vegetation, and some of this passes through the digestive system without being digested; in addition the dung contains various digestive juices, albuminous substances, fats, carbohydrates, mineral salts, vitamins, and also traces of other substances including bacterial albumens. The excreta of omnivores, e.g., man and pigs, is also often used, whereas droppings of carnivores are only occasionally visited. Through specialisation to particular ecological conditions, such as the abundance of rodents in the semi-deserts and deserts of the Old and New World, some species have become adapted to the use of the pellets of rodents. The indigenous Australian species of *Podotenus* (Stebnicka & Howden 1994, 1995) are attracted to human and bovine excreta; however, they mostly depend upon the pellet-like dung of marsupials. Some species are attracted in small numbers to carrion. The true coprophages include most species of Aphodiini, some Eupariini and Psammodiini, and some members of other tribes.

Generally, the climatic conditions of the environment and the microclimatic conditions of the soil restrict dung beetles to certain habitats. It is obvious that some adults of typical saprophages and coprophages have a mixed diet. For example, the adults of a given species imbibe the liquid that seeps from vegetable masses undergoing fermentation even though some individuals also occasionally consume the liquid contents of dung or exhibit other feeding habits, such as consuming various waste materials discarded by ants and termites.

The larvae of all species of aphodiines have mouthparts always of the biting type, and are able to process almost all kinds of food. Development takes place entirely in the soil, under or inside various kinds of dung, or in decaying vegetation. The females lay 20–25 eggs on average and do not look after their offspring. The majority of species have two generations per year, which means that their development cycle lasts less than a year. However, the emergence pattern is very variable and irregu-

lar, since the yearly number of generations in a given area depends on climate and on the duration of the growing season.

The distribution of many species has lost its continuous character, some of them are absent from the industrialised areas of the world. Chemicals penetrating the soil in rainwater exert a negative effect on the mortality of insects, especially at the earlier stages of development, and subsequently cause a restriction, or even total extinction of populations in a particular area.

## BIOGEOGRAPHY

The Aphodiinae have a bipolar geographical distribution with a few typically Laurasian tribes and several Gondwanan ones. There are also intermediate, relict tribes and genera. One of the two largest tribes, the Eupariini, is basically Gondwanan and saprophagous, whereas the Aphodiini are mostly coprophagous and are most conspicuous in temperate biomes of the northern hemisphere. It may be assumed that Aphodiinae have probably differentiated in Laurasia and Gondwana after the split up of Pangea. I suggest the beetles may then have diverged into two main sister groups, of which only the older, southern members of the Eupariini have retained a typical Gondwanan distribution. These groups may originally have had saprophagous feeding habits in tropical forests, where they probably turned to the dung of small primitive mammals that were forest dwellers (Cambefort 1991)

The current fauna of Aphodiinae in New Zealand consists of two elements: indigenous species, and species that have been accidentally introduced, mainly from Australia. How does this equate with the known distribution within and outside New Zealand of the species known from this country? Of the twenty species here recognised from New Zealand, nine are indigenous and it is possible to draw some conclusions from their systematic relationships.

### Species known outside New Zealand

The eleven species known also from outside New Zealand are as follows:

*Aphodius granarius* (L.) and *A. lividus* (Ol.). Cosmopolitan, anthropogenic species with a wide range of edaphic and climatic tolerances, transported from Europe to all continents by man. Their closest relatives of the subgeneric-groups *Calamosternus*, *Nialus*, and *Liothorax*, occur in the Palaearctic.

*Acrossidius tasmaniae* (Hope). Distributed in Australia and Tasmania, closely related to the other three Australian species of *Acrossidius* (Stebnicka & Howden 1995);

relationships of the species are unclear.

*Proctophanes minor* (Blackb.) and *P. sculptus* (Hope). Known from Australia and Tasmania, belong to a compact group of eight Australian species (Stebnicka & Howden 1995); their tribal relatives occur in Africa.

*Australaphodius frenchi* (Blackb.). Decidedly an affrotropical species introduced to Australia and Tasmania (Stebnicka & Howden 1995) and to Chile (new record); its congeners occur in Africa.

*Parataenius simulator* (Har.). Neotropical species introduced to various countries including Europe (Portugal), southeastern United States, and Australia; at least five closely related species of *Parataenius* occur in South America.

*Ataenius picinus* (Har.). Nearctic–Neotropical species, widely distributed throughout Pacific Islands to Australia; its close relatives occur in South and North America.

*Ataenius brouni* (Sharp). Species known from eastern Australia and Tasmania; it has clear affinities with the West Australian species *A. nudus* Blackburn.

*Saprosites mendax* (Blackb.). Australian species distributed in southeastern areas of Australia including Tasmania, introduced to Europe (England); it is close to the sympatric *S. nitidicollis* (Macleay).

*Tesarius sulcipennis* (Lea) [See Remarks at the description, p. 23]. A species known from Tasmania, most probably introduced to the Chatham Islands; its close relatives occur in Australia, e.g., *Leiopsammodius newcastleensis* Stebnicka & Howden (1996) described from sand dunes in New South Wales.

If we leave out of consideration the two cosmopolitan species of *Aphodius*, a Gondwana character is evident in the origin and distribution of all the species known outside New Zealand.

*Phycocus* and *Saprosites* both have indigenous species in New Zealand.

### Indigenous species

The monospecific genus *Phycocus* represents an old element and may be considered as a typical relict, widely distributed in New Zealand including the Chatham Islands and introduced to Tasmania. It seems likely that the monotypic genera are actual relicts of otherwise extinct lineages, whereas some of the other genera may represent polyphyletic lineages resulting in artificial assemblages of non-related species. *Phycocus graniceps* Broun shares some character states with *Tesarius sulcipennis* and *Leiopsammodius newcastleensis*, however, a possible convergence of characters complicates the question of affinities, for example, loss of hind wings with result-

ant morphological changes is common, as are obvious adaptations to similar habitat, in this case coastal sand dunes.

The genus *Saprosites* belongs to a group of related genera distributed in the Southern Hemisphere and containing the Neotropical *Passaliolla* Balthasar (Stebnicka 2000a) and *Iguazua* Stebnicka (1997), and the Asian–Australian *Cnematoplatys* Schmidt (Stebnicka & Howden 1997, Stebnicka 1998b). The New Zealand *Saprosites* species-group is morphologically very close to the tropical and subtropical groups of the genus. Based on morphological similarities and differences the New Zealand species can be split into two groups: (1) *exsculptus*, *distans*, and *raoulensis*; (2) *communis*, *fortipes*, *sulcatissimus*, *watti*, and *kingsensis*. Each group has probably evolved in New Zealand from a different ancestral colonising species. The members of group (1) appear to have close congeners in South America (Stebnicka 2001, in press), those of group (2) seem to have their closest relatives in Australia. The endemic species on the outlying islands share a large number of character states with those of the North and South Islands and are undoubtedly New Zealand derivatives.

*Saprosites* is seemingly one of the oldest taxa of Eupariini. Crowson (1981) assumed, that the archetypal coleopteran structure — a somewhat flattened form with relatively short legs, and non-projecting coxae and short antennae — is related to the style of insect life, with the species habitually taking refuge under loose bark of dead trees. The species of *Saprosites* live in moss, leaf litter, and in the dead, rotten trunks of many tree species. They are good examples of the “soft saphrophagy” life style, with adults probably feeding on the liquid fractions of rotten wood.

Since the more primitive species or groups are likely to retain the most primitive characters it is important to know where the most primitive forms are likely to be found. New Zealand and Australia with neighbouring archipelagos, and to a lesser degree, South America, are great reservoirs of primitive types. Outside of these areas primitive groups may be widely but discontinuously distributed, frequently with highly localised, distantly related species. The New Zealand fauna of Aphodiinae is closest to that of Australia with connections to the Pacific Islands, Indonesia, Southern India, East Africa, Madagascar, and South America. The oldest forms probably arrived in the present New Zealand before the opening of the Tasman Sea 80 million years ago, and in all probability in the late Jurassic after the Rangitata Orogeny, when the present New Zealand formed part of a greater land mass connected to the rest of Gondwana (Stevens 1980). In the Cretaceous New Zealand was joined to West Ant-

arctica (Marie Byrd Land) and fronted the broad Pacific, whereas Australia was joined to East Antarctica (Wilkes Land) and was situated in the lee of Africa–Madagascar–India. New Zealand thus became a big land mass connected to other parts of Gondwana, and could receive plant and animal immigrants from these sources. It has been forested throughout most of its history and has been an archipelago since the Late Cretaceous (Raven & Axelrod 1972). Much of New Zealand, which was previously forested, is now grassland, especially in the North Island. Clearing forest and converting it to pasture caused a local loss of the indigenous forest fauna (Watt 1977). It seems likely that the existing native species represent only a fraction of the ancient fauna. There was probably a great deal of extinction of warmth-adapted groups during the Pleistocene (Fleming 1975), and the New Zealand fauna of Aphodiinae may have been considerably less fragmented during the Tertiary than it is now. The gaps in distribution could indicate extinction resulting from climatic or geological changes, from contemporary destruction or severe modification of native habitats, or from unsuccessful competition with invading species.

## COLLECTING AND PREPARATION METHODS

Aphodiines are typically found on the ground, and may be obtained through searching beneath or in various kinds of dung, under objects such as plant debris, stones, and logs, and under loose bark of dead trees. Soft forceps can be used to pick up specimens. Individuals hide effectively in soil and debris if given the opportunity. Sifting leaf litter and riparian vegetation should produce members of groups such as *Phycocus*, *Ataenius*, and *Saprosites*. Pit-fall traps can be quite productive for some species, and flight-intercept traps work well for those with fully developed wings. The label data of the specimens indicate that numerous examples from New Zealand were collected by these means.

Specimens are usually placed into 70% ethanol, and stored until they are prepared. A few species in New Zealand genera are large enough to be pinned, but most should be glued on triangular points in the American style or mounted on cards with a water-soluble glue in the European style. Point-mounted specimens are recommended, particularly for the members of Eupariini. Examination of the ventral surface of the body is important to confirm identification or even for identification. It is often impossible to recognise males of *Ataenius* and *Saprosites* when they are mounted on cards. The male genitalia and the labro-epipharyngeal structures should be examined until

one is familiar with their subtle differences.

Preparation of aphodiines for dissection does not differ significantly from that for the other groups of beetles. The whole specimen should be placed in hot water for 15 minutes or boiled for at least 3 minutes, then placed in a small dish in a droplet of 70% ethanol. The male genitalia and labrum can be removed using a minute insect pin with a curved tip, grasped with a set of forceps, then placed into glycerol for clearing and examination. The parts may be stored in glycerol in a microcapsule pinned beneath the remounted specimen, or glued on a separate card using a water-soluble glue.

## CONVENTIONS

The two-letter code used at the beginning of records or in the summary of distribution refers to areas of New Zealand as defined by Crosby *et al.* (1998). Abbreviations of repositories are given through the text as follows:

- AMNZ Auckland Institute and Museum, Auckland, New Zealand (J. W. Early)
- ANIC Australian National Insect Collection, CSIRO, Canberra, A.C.T. Australia (J. F. Lawrence, T. A. Weir)
- BMNH The Natural History Museum, London, U.K. (M. D. Kerley)
- CMNO Canadian Museum of Nature, Ottawa, Ontario, Canada (H. F. Howden, F. Génier)
- CMNZ Canterbury Museum, Christchurch, New Zealand (C. A. Muir)
- DEIE Deutsches Entomologisches Institut, Eberswalde, Germany (L. Zerche)
- ISEA Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Cracow, Poland (Z. T. Stebnicka)
- LUNZ Lincoln University, Canterbury, New Zealand (R. M. Emberson, J. M. W. Marris)
- MHNG Muséum d'histoire naturelle, Geneva, Switzerland (I. Löbl, B. Merz, G. Cuccodoro)
- MNHN Muséum National d'histoire naturelle, Paris, France (Y. Cambefort)
- USNM National Museum of Natural History, Smithsonian Institution, Washington, U.S.A. (G. House)
- MONZ Museum of New Zealand Te Papa Tongarewa (formerly National Museum), Wellington, New Zealand (R. L. Palma)
- NMPC National Museum, Prague, Czech Rep. (J. Jelinek)
- NRSS Naturhistoriska Riksmuseet, Stockholm, Sweden (D. Borisch)
- NZAC N. Z. Arthropod Collection, Mt Albert Research

	Centre, Auckland, New Zealand (T. K. Crosby, R. A. B. Leschen)
HCOE	Hope Department of Entomology, Oxford University, Oxford (M. Atkinson)
OMNZ	Otago Museum, Otago, New Zealand (A. C. Harris, B. H. Patrick)
SAMA	South Australian Museum, Adelaide, South Australia, Australia (E. G. Matthews)
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany (W. Schawaller)
SMTD	Staatliches Museum für Tierkunde, Dresden, Germany (D. Ahrens)

## KEY TO APHODIINAE KNOWN FROM NEW ZEALAND

- 1 Body globular; metatibia broad, apical spurs spatulate, tarsus extremely short ..... (Psammodiini) ... 2  
 —Body elongate; metatibia slender, apical spurs spiniform, tarsus long or moderate in length ..... 3
- 2(1) Pronotum very short, smooth lacking punctures; elytra smooth without striae or with slight traces of striae; metatibia with irregularly spaced denticles on outer side (Fig. 30) (p. 21) ... *Phycocus graniceps* Broun  
 —Pronotum moderate in length, slightly swollen, with transverse rows of punctures; elytra with impressed, punctate striae; metatibia with strong transverse ridge on outer side (Fig. 31) ..... (p. 22) ... *Tesarius sulcipennis* (Lea)
- 3(1) Abdominal sternites with intersegmental membranes; pygidium covered by elytra without scabrous area basally (Fig. 26); apical spurs of metatibia separate, located on each side of tarsal insertion (Fig. 28) ..... (Aphodiini) ... 4  
 —Abdominal sternites coalesced, usually grooved along sutures; pygidium partially exposed with scabrous area basally (Fig. 27); apical spurs of metatibia located close together below tarsal insertion (Fig. 29) ..... (Proctophanini, Eupariini) ... 6
- 4(3) Large, 9.0–14.0 mm long; head with obtuse tubercle behind middle of frontal suture; pronotum with lateral fringe of long, close setae (Fig. 1) ..... (p. 20) ... *Acrossidius tasmaniae* (Hope)  
 —Small, 3.5–5.0 mm long; head with three, more or less elevated tubercles on frontal suture; pronotum laterally with few short setae or lacking setae ..... (Aphodius) ... 5
- 5(4) Ground colour pale yellow with smoky brown areas on pronotum and elytra; base of pronotum without marginal line (p. 19) ... *Aphodius lividus* (Olivier)  
 —Colour black, sometimes tinged with brown; base of pronotum with distinct marginal line ..... (p. 18) ... *Aphodius granarius* (Linnaeus)
- 6(3) Middle of head weakly convex, frequently with transverse carina or tubercles; elytra lacking basal bead; transverse ridges of metatibia strongly developed ..... (Proctophanini) ... 7  
 —Middle of head strongly gibbose without transverse carina; elytra with basal bead; transverse ridges of metatibia absent or distinctly reduced ..... (Eupariini) ... 9
- 7(6) Pronotal base straight with distinct marginal line, surface with fine, uniform, evenly spaced punctures; exposed portion of pygidium with long pale setae, lacking longitudinal carina ..... (p. 25) ... *Australaphodius frenchi* (Blackburn)  
 —Pronotal base lobed at middle without marginal line, surface punctures mixed, minute and large, unevenly spaced; exposed portion of pygidium with longitudinal carina, lacking setae ..... (Proctophanes) ... 8
- 8(6) Size moderate, 5.0–5.8 mm long; frontal suture with more or less elevated transverse tubercles; elytral striae as wide as intervals, with transverse, coarse punctures (p. 23) ... *Proctophanes sculptus* (Hope)  
 —Size small, 3.2–3.8 mm long; frontal suture not indicated, lacking tubercles; elytral striae narrower than intervals, with round, fine punctures ..... (p. 24) ... *Proctophanes minor* (Blackburn)
- 9(6) Head with coarse, transverse granules; metatibia strongly expanded at apex, apical spurs slightly sinuate ..... (p. 26) ... *Parataenius simulator* (Harold)  
 —Head never granulate; clypeal surface slightly wrinkled, punctate or impunctate; metatibia moderately expanded at apex, apical spurs straight ..... 10
- 10(9) Head much narrower than pronotum; pronotum transverse; elytral disc more or less convex, 10th elytral interval wider than 9th interval ..... (Ataenius) ... 11  
 —Head almost as wide as pronotum; pronotum subquadrate; elytral disc flattened, 10th elytral interval as wide as 9th interval or narrower ..... (Saprosites) ... 12



- 11(10) Length 4.8–6.0 mm; clypeal surface slightly wrinkled; pronotal punctures unequal in size, coarser punctures lacking in anterior median area; metatibia without traces of transverse ridges ..... (p. 28) ... *Ataenius picinus* **Harold**  
—Smaller, 3.0–4.0 mm long; clypeal surface punctate; pronotal punctures equal in size, everywhere spaced; metatibia with traces of transverse ridges ..... (p. 27) ... *Ataenius brouni* **(Sharp)**
- 12(10) Length exceeding 4.5 mm ..... 13  
—Length less than 4.0 mm ..... 15
- 13(12) Basal pronotal angulation not prominent; elytron with conical, sharply pointed humeral denticle, punctures of elytral striae moderate in size; metatibia relatively long, basal segment of metatarsus equal to length of upper tibial spur ..... (p. 32) ... *Saprosites distans* **(Sharp)**  
—Basal pronotal angulation prominent; elytron with trap-ezoid, obtuse humeral denticle, punctures of elytral striae large; metatibia relatively short, basal segment of metatarsus much shorter than upper tibial spur ... ..... 14
- 14(13) Elytral intervals flattened on disc, about 2× as wide as striae; meso- and metatibia robust with strong accessory spines ..... (p. 31) ... *Saprosites exsculptus* **(White)**  
—Elytral intervals convex on disc, about 1.5× as wide as striae; meso- and metatibia slender with small accessory spines ..... (p. 33) ... *Saprosites raoulensis* **(Broun)**
- 15(12) Posterior angles of pronotum distinctly excavate before prominent basal angulation, pronotal punctures mixed, minute and fine ..... (p. 30) ... *Saprosites mendax* **(Blackburn)**  
—Posterior angles of pronotum broadly rounded toward base, basal angulation lacking, pronotal punctures mixed, minute and large ..... 16
- 16(15) Pronotal base with row of punctures, without marginal line; elytral intervals 7 and 9 united at middle of elytral length with 8th interval very short (Fig. 24) ..... (p. 35) ... *Saprosites fortipes* **(Broun)**  
—Pronotal base with more or less distinct marginal line frequently crenated by punctures; elytral intervals 7 and 9 united at apical third of elytral length with 8th interval shorter than adjacent intervals (Fig. 25). 17
- 17(16) Elytral intervals on disc strongly convex, nearly as wide as striae, striae punctures weakly crenating inner margins of intervals ..... (p. 37) ... *Saprosites sulcatissimus* **(Broun)**  
—Elytral intervals on disc slightly convex or flattened, somewhat wider than striae, striae punctures distinctly crenating inner margins of intervals ..... 18
- 18(17) Head strongly gibbose medially, gena very small, obtuse; pronotum with lateral and basal margins smooth; elytra slightly arcuate toward apex, humeral denticles small ..... (p. 36) ... *Saprosites watti* **n.sp.**  
—Head moderately gibbose medially, gena right-angled, prominent; pronotum with lateral and/or basal margin more or less distinctly crenate; elytra parallel-sided, humeral denticles large, prominent ..... 19
- 19(18) Posterior pronotal angles distinctly crenate-serrate, disc usually with median longitudinal line of contiguous punctures; elytra usually about 2.5× as long as pronotum (p. 33) ... *Saprosites communis* **(Broun)**  
—Posterior pronotal angles smooth or minutely crenate, disc without median longitudinal line of contiguous punctures; elytra usually 2× as long as pronotum or slightly longer (p. 34) ... *Saprosites kingsensis* **n.sp.**

## DESCRIPTIONS

### Subfamily Aphodiinae

#### Tribe Aphodiini

#### Genus *Aphodius* Illiger

*Aphodius* Illiger, 1798: 15, et auctt. Type species *Scarabaeus fimetarius* Linnaeus, 1758: 348, by subsequent designation of Latreille (1810).

Length 1.5–16.0 mm. Upper surface of body glabrous, minutely setigerous or only elytra covered with distinct setae.

Head variously shaped and sculptured; clypeo-frontal suture tuberculate or not, antennal club circular, ovoid, or elongate.

Pronotum usually rectangular, evenly convex, with or without basal marginal line. Scutellum from small to very large, triangular, pentagonal, semi-oval, or cordate.

Elytra without basal bead and preapical umbone; elytral intervals smooth, alternately not differentiated; metathoracic wings developed or reduced in various degree (brachypterous), or absent.

Abdominal sternites not fused, with intersegmental membranes. Pygidium as Fig. 26.

Legs moderate in length to long; meso- and metatibia usually widened toward apex, transverse ridges more or less clearly developed, apical fringe composed of close setae of various lengths; apical spurs of metatibia separated, located on each side of tarsal insertion.

Male genitalia mostly sclerotised; phallobase with hump, apices of parameres variously shaped, internal sac with narrow, membranous or lightly sclerified apical portion, sometimes with group of fine spicules.

External sexual differences apparent in sculpture of head and pronotum, occasionally in the shape of protibia and its terminal spur.

**Remarks.** *Aphodius* is a very large genus, most diverse in the Northern Hemisphere, penetrating to a limited extent into Ethiopian and Neotropical regions. It contains approximately 1800 species divided into 135 subgenera. Most of the species live in open forest clearings, pastures, and meadows. They are found in various areas from lowlands to 5000 m above sea level (Himalayas: Stebnicka 1986, 1989, 1990; Ahrens & Stebnicka 1997). *Aphodius* is poorly represented in Australian region and includes several introduced species. Two cosmopolitan species of this enormous genus are known to be established in New Zealand.

### *Aphodius (Calamosternus) granarius* (Linnaeus)

Fig. 7, 33, 44, Map 1

*granarius* Linnaeus, 1767: 9 (*Scarabaeus*); —Erichson 1848: 813 (*Aphodius*); —Reitter 1892: 189 et auctt. (*Aphodius (Calamosternus)*); —Hutton 1898: 156 (*Aphodius*); —Hudson 1923: 374; —Watt, 1984: 8–9; —Dellacasa 1988: 134 (catalogue) (*Aphodius (Calamosternus)*); —Cassis & Weir 1992: 88 (catalogue); —Stebnicka & Howden 1995: 714, Fig. 70, 109.

*adelaide* Hope, 1846: 146 (*Aphodius*); —Harold 1863: 342 (as synonym of *granarius*).

Length 3.5–5.0 mm. Body subparallel-sided, shining, colour black to dark brown, sometimes elytra lighter than head and pronotum.

Head moderate in size, clypeal margin rounded on each side of shallow median emargination, sides arcuate toward rounded, prominent gena; clypeal surface slightly rugosely punctate, usually with transverse carina just above median emargination, frontal suture with 3 more or less elevated tubercles. Epipharyngeal structures as in Fig. 33.

Pronotum convex, sides and base with marginal line, surface punctures mixed, fine and moderate, irregularly spaced and widely scattered. Scutellum slightly pentagonal with few punctures, or impunctate.

Elytra parallel-sided, moderately convex, striae impressed and punctate, intervals flat with minute scattered punctures, or impunctate.

Abdominal sternites rugulose, more closely punctate on sides, each with row of short pale setae.

Legs moderate in length; transverse ridges of meso- and metatibia well developed; apex of metatibia with short, close setae, basal segment of metatarsus equal in length to upper tibial spur or slightly shorter and equal to following 2 tarsomeres combined.

Male. Frontal tubercles more elevated than in female, pronotum more convex; genitalia as in Fig. 44.

Female. Punctures of pronotum usually closer than in male.

**Type data.** *Aphodius granarius*: type material (“Europae”) presumed to be in the collection of the Linnean Society, London.

*Aphodius adelaide*: described from South Australia, Adelaide. Lectotype (HCOE) designated by Stebnicka & Howden (1995).

**Material examined.** Lectotype of *A. adelaide* plus 57 non-type examples (AMNZ, ISEA, LUNZ, MONZ, NZAC).

ND, AK, CL, WO, BP, HB, TK, WI, WN / NN, MB, KA, NC, MC, SL / CH

Collected August–January, March.

Recorded from near sea level.

Ecologically very tolerant, feeding on debris, decaying vegetation, compost, carrion, and on various kinds of dung; collected at light. In New Zealand found primarily in compost heaps and soil, Chathams specimens were found in sheep and cow dung.

**Remarks.** *Aphodius granarius* is similar in general appearance to *Australaphodius frenchi* and is often misidentified in collections. It differs from *A. frenchi* in having the head tuberculate, the pronotum irregularly punctate, and the apical spurs of metatibia separate, located on each side of the tarsal articulation. A cosmopolitan species, its close relatives occur in the Palaearctic. The earliest definite New Zealand record is Hutton (1898), who reported it from the Chatham Islands and Canterbury. Chatham Islands specimens are present in the Hutton Collection (CMNZ). According to Watt (1984) there is also an undated Broun specimen labelled “Tairua” probably collected before he left there in 1877. The preimaginal stages have been described by Jerath (1960).

***Aphodius (Nialus) lividus* (Olivier)**

Fig. 34, 45, Map 2

*lividus* Olivier, 1789: 86 (*Scarabaeus*); —Harold 1871: 258 (*Aphodius*); —Reitter 1892: 202 et auctt. (*Aphodius (Nialus)*); —Stebnicka & Howden 1995: 714–716, Fig. 71, 110; —Stebnicka 1998b: 836.

*cincticulus* Hope, 1847: 284 (*Aphodius*); —Schmidt 1922: 316 (as synonym of *lividus*).

*spilopterus* Germar, 1848: 189 (*Aphodius*); —Schmidt 1922: 316 (as synonym of *lividus*).

*pseudolividus* Balthasar, 1941a: 148 (*Aphodius (Nialus)*); —Petrovitz 1961: 105; —Brown 1967: 43 (*Aphodius*); —Watt 1984: 7; —Dellacasa 1988: 154 (catalogue) (*Aphodius (Labarrus)*); —Cassis & Weir 1992: 89 (catalogue); —Bordat et al. 1990: 36; —Paulian 1991: 86; —Stebnicka & Howden 1995: 714 (as synonym of *lividus*).

*lividus pseudolividus*: Endrödi & Rakovič, 1981: 47 (*Aphodius (Nialus)*); —Cartwright & Chalumeau 1978: 7.

Length 4.0–5.2 mm, greatest width 1.5–1.8 mm. Body elongate oval, shining, ground colour pale yellow with smokey brown areas on pronotum and elytra.

Head moderate in size, clypeal margin rounded on each side of median emargination, slightly arcuate towards small, rounded gena, anterior edge fringed with extremely short setae; frontal suture with three more or less elevated tubercles, punctures of head fine, variable in density. Epipharyngeal structures as in Fig. 34.

Pronotum transverse; lateral edge finely margined, base without marginal line; surface punctures variable, minute to fine, punctures more or less clearly visible, larger punctures scattered, usually more concentrated on each side of disc. Scutellum subtriangular, slightly concave medially or not concave.

Elytra convex with fine striae, strial punctures fine to moderate in size, slightly crenating margins of intervals; intervals almost flat, very finely punctate or impunctate, sometimes punctures more distinct at apex.

Ventral surface shiny; abdominal sternites punctate from side to side, with 1–2 rows of pale setae; metasternum slightly concave in both sexes or only in male.

Legs moderate in length, transverse ridges of meso- and metatibia well developed; basal segment of metatarsus slightly widened at apex or not widened, equal in length or slightly shorter than upper tibial spur and subequal in length to following 2 tarsomeres combined.

Male. Pronotum usually wider and more convex than in female, punctures scarcer; genitalia as in Fig. 45.

Female. Penultimate abdominal sternite usually longer than in male.

**Type data.** *Aphodius lividus*: described from France, vicinity of Paris. Type material in MNHN.

*Aphodius cincticulus*: described from Australia, Adelaide. Type material in HCOE.

*Aphodius spilopterus*: described from Australia, Adelaide. Location of type material unknown.

*Aphodius pseudolividus*: described from South America. Type material in Balthasar Collection (NMPC).

**Material examined.** Holotype of *A. pseudolividus* and 45 non-type specimens (AMNZ, ISEA, LUNZ, MONZ, NZAC).

ND, AK, CL, WO, BP, GB, WI, WN / SD, NN.

Collected October to May.

Recorded from sea level to near 500 m.

A species with a wide range of edaphic and climatic tolerances, found in soil near rabbit burrows, in various kinds of dung, and commonly collected at light. In New Zealand it is found primarily in cattle and sheep dung and collected at light.

**Remarks.** This species is easily distinguishable by its yellow body with various shades of brown. The *Aphodius lividus* complex has been divided by Petrovitz (1961) into ten species on the basis of their allopatric distribution. Because *A. lividus* shows a polymorphic pattern, especially as far as male genitalia are concerned, the synonymy is fairly extensive. Cosmopolitan, a very variable species with its close relatives occurring in the Palaearctic. The earliest New Zealand record is Karekare (AK), Feb. 1916, A.E. Brookes (NZAC) (Watt 1984).

**Genus *Acrossidius* Schmidt**

*Aphodius (Acrossidius)* Schmidt, 1913: 135. Type species *Aphodius tasmaniae* Hope, by subsequent designation of Balthasar (1964).

Length 9.0–14.0 mm. Body with entire dorsum glabrous or elytra sparsely to densely covered with minute to short setae.

Head with or without transverse tubercle above clypeofrontal suture; antennal club circular or ovoid.

Pronotum rectangular or subquadrate, posterior angles more or less broadly rounded, lateral margins fringed with long, pale hairs, basal marginal line lacking.

Elytra without basal bead and preapical umbone; elytral intervals shining, not alternately differentiated. Metathoracic wings well developed.

Abdominal sternites not fused, sutures slightly convex.

Legs long; each lateral tooth of protibia with tuft of long yellow setae on each side; meso- and metatibia widened toward apex, transverse ridges feebly developed; apical setae thick, very long with shorter setae intermixed;

upper apical spur of metatibia approximate to lower one, both located on inner tibial margin and separated from tarsal insertion.

Male genitalia strongly sclerotised, phallobase without hump, dorsal membrane of parameres terminating in variably elongate process; apical portion of internal sac widened with sclerites and close spicules.

External sexual differences apparent in the shape and sculpture of head, pronotum, elytra, and protibia and in the length of metatarsal tarsomeres.

**Remarks.** This native Australian genus includes four species, two of which are restricted to South Australia and one to Tasmania. *Acrossidius tasmaniae* is the most widely distributed species, and introduced into New Zealand.

### ***Acrossidius tasmaniae* (Hope) Tasmanian grass grub**

Fig. 1, 35, 46, Map 3

*tasmaniae* Hope, 1847: 285 (*Aphodius*); —Schmidt 1913: 135 (*Aphodius* (*Acrossidius*)); —1922: 127; —Given 1958: 196; —Watt 1970: 11; —1984: 7, fig. 1; —Dellacasa 1988: 206 (catalogue); —Cassis & Weir 1992: 86 (catalogue); —Stebnicka & Howden 1995: 726–727, Fig. 18–20, 81, 17 (*Acrossidius*).

*howitti* Hope, 1847: 285 (*Aphodius*); — Schmidt 1913: 135 (*Aphodius* (*Acrossidius*)); —1922: 128; —Given 1950: 153 (as synonym of *tasmaniae*).

*longitarsus* Redtenbacher, 1867: 58 (*Aphodius*); —Schmidt 1910: 88 (as synonym of *tasmaniae*).

*andersoni* Blackburn, 1904: 154 (*Aphodius*); —Given 1950: 153 (as synonym of *tasmaniae*).

*pallidihirtus* Balthasar, 1941b: 163 (*Aphodius* (*Acrossidius*)); —Stebnicka & Howden 1995: 726–727 (as synonym of *tasmaniae*).

Length 9.0–14.0 mm, greatest width 4.0–5.5 mm. Body yellow, reddish brown, to black, in dark specimens sides of pronotum lighter.

Head large; clypeal margin upturned, truncate anteriorly; frontal suture transversely convex near eyes; tubercle behind frontal suture usually distinct. Epipharyngeal structures as in Fig. 35.

Pronotum with sides margined, fringed with long, pale setae.

Elytra with striae impressed, finely punctate; intervals convex with fine to moderate punctures in rows along striae.

Legs slender; transverse ridges of meso- and metatibia flat, incomplete.

Male. Head semicircular, surface punctures fine, uniformly spaced. Pronotum moderately to strongly convex, wider than elytra, sometimes with slight longitudinal line medially; surface punctures minute to fine, scattered.

Elytra parallel-sided with short, sparse setae in apical 1/3; punctures of elytral intervals shallow. Legs long; lateral teeth of protibia widely separated with smaller intervening teeth; terminal spur robust, rounded apically, bent downward; basal segment of metatarsus slightly shorter than upper tibial spur and equal to following three tarsomeres combined; genitalia as in Fig. 46.

Female. Head smaller than in male, sides slightly converging anteriorly; clypeal margin usually weakly emarginate; tubercle behind frontal suture flattened but distinct; surface punctures markedly larger and deeper than in male, most separated by their diameter. Pronotum as wide as elytra, punctures the same size as those of head, separated by about 1–3× their diameter. Elytra widened toward apex with very fine, often barely visible, scattered setae on apical declivity; punctures of elytral intervals often coarser than in male. Lateral teeth of protibia approximate, terminal spur sharply pointed; basal segment of metatarsus 1/3 shorter than upper tibial spur and equal or subequal to following 2 tarsomeres combined.

**Type data.** *Aphodius tasmaniae*: described from Tasmania. The holotype could not be found in the HCOE; location unknown.

*Aphodius howitti*: described from Port Phillip [Australia]. Lectotype (HCOE) designated by Stebnicka & Howden (1995).

*Aphodius andersoni*: described from Australia. Lectotype (HCOE) designated by Stebnicka & Howden (1995).

*Aphodius pallidihirtus*: described from Mt Gambier [Australia]. Type material in Balthasar Collection (NMPC).

**Material examined.** Type specimens of *A. howitti*, *andersoni*, and *pallidihirtus* plus 235 non-type examples (AMNZ, CMNZ, ISEA, LUNZ, MONZ, NZAC).

ND, AK, CL, BP, RI, WN / MB, KA, NC, MC, SC.

Collected November to March.

Recorded from near sea level.

It is common in coastal mid-Canterbury (Lowe 1961) damaging pastures, and also reported from the Auckland area (May 1961). Found in pastures, in rabbit middens; collected primarily at light during warm summer evenings, occasionally under vegetation, e.g., under *Cassinia*. According to Brown (1967), the first New Zealand record is a specimen from Mt Grey, Canterbury, 1916 (CMNZ).

**Remarks.** This is one of the most highly variable species of Aphodiini. Morphological variants fall into three groups: sexual dimorphism, allometric or heterogonic

growth, and geographic variation. The main sexual characters are included in the description. The second type of variation, related to nutrition and size, is expressed in both sexes. Generally stated, larger males have a wide, semicircular head with a pronounced tubercle and a robust, strongly convex pronotum that is wider than the elytra. As body size decreases so does the relative size of the head and pronotum. In larger females the median tubercle of the head is well developed, the punctures of the pronotum are moderately dense, and the elytra are widened toward apex and distinctly pubescent on the apical declivity. Geographic variation is expressed in colour and in the punctuation of the body, e.g., specimens collected in mountainous areas are often melanistic or black, whereas specimens from lowland areas are lighter in colour, usually being various shades of brown. The series of New Zealand specimens (NZAC) found in rabbit middens at Hathaway, Clarence (KA) are yellow in colour.

*Acrossidius tasmaniae* occurs in New Zealand, Tasmania, and from the Eyre Peninsula through southeastern South Australia, Victoria to eastern New South Wales. It is most closely related to the sympatric *A. pseudotasmaniae* (Given) and known as the blackheaded pasture cockchafer, a common pasture pest. Larvae of *A. tasmaniae* are unusual among Aphodiini in feeding on grass and clover leaves. According to Wightman (1979), Watt (1984), and Emberson & Stephenson (1999), the leaves are dragged down into the tunnels in the soil and eaten there. Light, well-drained soils are favoured.

### Tribe Psammodiini

#### Genus *Phycocus* Broun

*Phycocus* Broun, 1883: 299. Type species *Phycocus graniceps* Broun, by original monotypy.

*Phycochus*: Broun 1886: 770, subsequent misspelling.

Body globular, strongly convex, glabrous above.

Head convex medially, anterior part granulate, vertex smooth.

Pronotum short, strongly transversal, evenly convex, lateral fovea slightly indicated. Scutellum small, triangular.

Elytra nearly circular without basal bead; striae absent or inconspicuously indicated.

Mesosternum and metasternum very short; abdomen gibbose at middle.

Legs short; mesocoxae contiguous; posterior trochanters long; femora short; metatibia strongly enlarged, on outer side furnished with unevenly spaced denticles, apical spurs equal in length, spatulate; claws hairlike (Fig. 30).

**Remarks.** This native New Zealand genus includes only one blind and flightless species that has been probably introduced to Tasmania.

#### *Phycocus graniceps* Broun

Fig. 2, 36, 47, Map 4

*graniceps* Broun, 1883: 300; —1886: 770; —Lea 1904: 90; —Schmidt 1922: 522; —Landin 1960: 62, fig. 4 F–L; —Brown 1967: 44; —Harris 1970: 1, Fig. 7, 9–11, 14; —Rakovi.. 1981: 32–33, 36, Fig. 12, 55–60; —Watt 1984: 13; —Dellacasa 1988: 307 (catalogue); —Cassis & Weir 1992: 103 (catalogue); —Stebnicka & Howden 1996: 109.

*lobatus* Broun, 1893: 1114; —Schmidt 1922: 523; —Rakovi... 1981: 36; —Watt 1984: 13 (as synonym of *graniceps*).

Length 2.5–3.0 mm, greatest width 2.0–2.2 mm. Colour shiny black, brownish black or brown, legs and ventral surface usually lighter.

Head convex, clypeal margin obtuse or subangulate on each side of narrow, deep median emargination, sides slightly arcuate or straight, in some specimens slightly emarginate before small, feebly prominent gena; clypeal surface granulate, frontal suture weakly marked, vertex smooth, polished. Eye absent. Epipharyngeal structures as in Fig. 36.

Pronotum short, strongly transversal, sides rounded, lateral margin distinctly crenate, base with marginal line; surface evenly convex, impunctate, usually with lateral fovea more or less indicated. Scutellum triangular, very small.

Elytra ovoid, strongly convex, without basal bead; humeral umbone and humeral denticle absent; elytron smooth or with slight traces of striae. Metathoracic wings absent.

Ventral surface shining; mesosternum and metasternum extremely short; abdomen gibbose medially with six visible sternites; sternites coalesced, setigerous; pygidium with long setae.

Profemur parallel-sided, as wide as metafemur; metafemur broad, 2× wider than mesofemur with few coarse punctures bearing pale setae; metatrochanter long; protibia with lateral teeth rounded apically, slightly transparent; metatibia 2× wider than mesotibia, outer side of metatibia with irregularly spaced denticles bearing short seta; tarsus very short, tarsomeres triangular, claws hairlike.

No external sexual differences visible; male genitalia as in Fig. 47.

**Type data.** *Phycocus graniceps*: Lectotype (sex undetermined) labelled “N Whangarei Harbour”, “*Phycochus graniceps*”, “New Zeal. Broun Coll. Brit. Mus. 1922–482” (BMNH) here designated.

*Phycocus lobatus*: Lectotype male, labelled "Taranaki", "*Phycoccus lobatus*", "New Zeal. Broun Coll. Brit. Mus. 1922-482" (BMNH) here designated.

**Material examined.** Type specimens plus 67 non-type examples (AMNZ, ANIC, ISEA, LUNZ, MONZ, NZAC, OMNZ).

ND, AK, WI, WN / NN, BR, MC, DN, OL, FD / CH. Collected January–April and August–November.

Recorded at or near sea level.

Strongly associated with coastal sand dunes on beaches, nocturnally active, commonly found beneath debris and under logs on the beach or in sand dune areas (Harris 1970, Watt 1984).

**Remarks.** This is the sole representative of the genus, indigenous to New Zealand and widely distributed, and is introduced to Tasmania (Hobart). It shares some character states with *Tesarius sulcipennis* and *Leiopsammodius newcastleensis* Stebnicka & Howden (1996) described from sand dunes in New South Wales. Unusual generic characters that distinguish *P. graniceps* from the other two genera are: pronotum extremely short and transverse, evenly convex without furrows or their vestiges; elytra non striate, without basal bead; posterior trochanters elongate.

### Genus *Tesarius* Rakovi...

*Tesarius* Rakovi., 1981: 27–29. Type species *Phycoccus sulcipennis* Lea, by monotypy.

Body globular, strongly convex, glabrous above.

Head convex medially, anterior part granulate, vertex smooth.

Pronotum rectangular, surface slightly swollen with rows of moderate punctures along transverse impressions. Scutellum small, triangular.

Elytra ovoid, strongly convex with basal bead and with 10 punctate striae.

Mesosternum and metasternum very short; abdomen convex at middle.

Legs short; mesocoxae contiguous; posterior trochanters moderate in length; femora short; metatibia broad with strong transverse carina on outer side, apical spurs spatulate, nearly equal in length; claws hairlike (Fig. 31).

**Remarks.** Rakovi. (1984) transferred four Nearctic, Pacific Coast species of *Psammodius* Fallén to the genus *Tesarius* on the basis of one character only, in this case the presence of transverse carina on the metatibia. The adaptive and mostly convergent characters of the legs are

obvious and complicate the question of monophyletic derivation of the Australian and Nearctic species. However, the phylogeny of Psammodiini in a general context is beyond the scope of this monograph.

### *Tesarius sulcipennis* (Lea)

Fig. 8, 48, Map 5

*sulcipennis* Lea, 1904: 89 (*Phycoccus*); —Schmidt, 1922: 523; —Landin 1960: 65 (*Phycoccus (Brindalus)*); —Rakovi. 1981: 27–29, Fig. 52–54 (*Tesarius*); —1984: 450; —Dellacasa 1988: 307 (catalogue); —Cassisi & Weir 1992: 103 (catalogue); —Stebnicka & Howden 1996: 109.

Length 2.8–3.2 mm, greatest width 2.1–2.2 mm. Body strongly convex, shiny; colour reddish brown to brownish black, legs and ventral surface usually lighter.

Head convex, clypeal margin obtuse to subangulate on each side of narrow, deep median emargination, sides straight or slightly emarginate before feebly protruding, setaceous gena; clypeal surface granulate, frontal suture weakly marked, vertex smooth, impunctate. Eye vestigial. Epipharyngeal structures similar to those in *Phycoccus graniceps* (Fig. 36).

Pronotum convex, distinctly wider than long, side margins fringed with pale hairs, basal edge crenate by punctures; pronotal surface slightly swollen with vestiges of transverse furrows marked by irregular rows of moderate to coarse punctures. Scutellum small, impunctate.

Elytra ovoid, strongly convex with basal bead and distinct humeral denticles, humeral umbone absent; elytron with 10 distinctly impressed striae, medium-sized punctures slightly crenating inner margins of intervals; intervals moderately convex, surface punctures minute, scattered, or lacking. Metathoracic wings absent.

Ventral surface shiny with scarce pale hairs; mesosternum and metasternum extremely short; abdomen convex medially with six visible sternites; sternites with single row of punctures bearing pale setae, pygidium with long setae.

Profemur rather narrow, equal to width of mesofemur; metafemur 2× as wide as mesofemur with few coarse punctures at apex; protibia with lateral teeth rounded apically, slightly transparent; metatibia nearly 2× wider than mesotibia with strong transverse carina on outer side; tarsus very short, metatarsal tarsomeres triangular, claws very fine, hairlike.

External sexual differences slight, elytra in male usually more rounded laterally than in female. Male genitalia as in Fig. 48.

**Type data.** Described from Tasmania. Lectotype (SAMA) and four paralectotypes (SAMA) designated by Rakovi. (1981).

**Material examined.** Type specimens plus 2 non-type examples (LUNZ).

– / – / CH.

Collected in January 1999 on Te One Beach.

Strongly associated with coastal sand dunes on beaches, found on sand dunes in late evening.

**Remarks.** *T. sulcipennis* is reported from New Zealand for the first time; it is distinct in its combination of globular body, slightly swollen pronotum and broad metatibia with transverse carina. This species shares many character states with *Leiopsammodius newcastleensis* (see Remarks under *Ph. graniceps*) and with other Australian species of the genus *Leiopsammodius* Rakovi. The shared characters of *T. sulcipennis* and *L. newcastleensis* are: body globular, head granulate, vertex smooth, eye and wings reduced; pronotum swollen with vestiges of transverse furrows; metasternum short, posterior trochanters not elongate; metatarsus very short, tarsomeres triangular, claws hairlike.

### Tribe Proctophanini

#### Genus *Proctophanes* Harold

*Proctophanes* Harold, 1861: 111. Type species *Aphodius sculptus* Hope, by monotypy.

Length 2.8–6.2 mm. Body short, oval, glabrous above; colour black to castaneous, sometimes head and pronotum black and elytra lighter.

Head usually slightly convex at middle, rarely carinate and tuberculate; clypeus emarginate and often slightly concave medially.

Pronotum subquadrate with tumosity laterally, base without marginal line, disc frequently with partial or complete median longitudinal impression. Scutellum triangular, acute apically.

Elytron with 10 striae including marginal one; intervals not alternately differentiated, epipleura very narrow.

Abdomen with sternites frequently fluted along sutures, penultimate sternite arcuate ventrally, pygidium exposed in apical 2/3 or in apical 1/2, finely grooved at base, usually with median longitudinal carina and/or lateral concavities.

Legs short; mesocoxae moderately separated with flattened or elevated carina between; protibia tridentate; meso- and metatibia expanded toward apex, transverse ridges fully developed, apical setae short; apical spurs slender, slightly curved, placed close together below tarsal insertion; tarsus short, tarsomeres subtriangular, claws hornlike.

**Remarks.** Members of *Proctophanes* occur in Australia, in Tasmania, and the Moluccas. The genus includes eight described species (Stebnicka & Howden 1995), two of which have been introduced to New Zealand.

#### *Proctophanes sculptus* (Hope)

Fig. 3–6, 9, Map 6

*sculptus* Hope, 1846: 147 (*Aphodius*); —Harold 1861: 111 (*Proctophanes*); —Schmidt 1910: 95. 1922: 364; —Dellacasa 1988: 196 (catalogue); —Cassis & Weir 1992: 93 (catalogue); —Stebnicka & Howden 1995: 744–745, Fig. 51–52, 98, 121.

Length 5.0–5.8 mm, greatest width 2.6–2.8 mm. Body robust, shiny, piceous black.

Head with clypeal margin reflexed, broadly rounded on each side of deep median emargination, sides slightly excised before small, obtuse gena; surface of head slightly roughly punctate with arcuate, transverse carina anteriorly, and with more or less elevated, transverse frontal tubercles.

Pronotum convex, sides finely margined, posterior angles rounded, base usually crenated by moderate punctures; median longitudinal furrow of pronotum more or less distinct, closely punctate, disc with mixed minute and moderate to large punctures, usually irregularly spaced. Scutellum triangular, larger than average, closely punctate at base.

Elytra widest at middle, humeri inconspicuously dentate or rounded; elytral striae deep, wide, alutaceous inside, on disc usually as wide as intervals, at apex wider than intervals and parallel; striae punctures transverse, close, distinctly crenating margins of intervals; intervals elevated on disc, subcarinate apically, surface shiny, minutely punctate.

Mesocoxae separate; metasternum convex, midline impressed, surface punctures fine, dense; abdominal sternites finely, closely punctate with short setae; pygidium exposed in apical 2/3, in both sexes with narrow, longitudinal, smooth carina at middle, surface alutaceous, subgranulate, apical lip narrowly shining.

Legs short; all femora wide with fine punctures and each with a row of setae; meso- and metatibia enlarged at apex; tarsus as long as tibia or a little shorter; basal segment of metatarsus slightly shorter than upper tibial spur and subequal to following 3 tarsomeres combined.

Male. Clypeal transverse carina and frontal tubercles usually much more elevated than in female, pronotum more convex; disc of metasternum slightly concave medially; genitalia as in Fig. 5.

Female. Body usually larger than in male, punctures of pronotum denser.

**Type data.** Described from southeastern Australia (Port Phillip); lectotype and paralectotype (HCOE) designated by Stebnicka & Howden (1995).

**Material examined.** Type specimens and 41 non-type examples (AMNZ, MONZ, NZAC).

ND, AK, BP, GB, TK, HB, WN / –.

Collected January–March, May–June, August–December.

Recorded from near sea level.

Most commonly found in cattle and horse dung and in marsupial droppings.

**Remarks.** *P. sculptus* is recognisable by its short, robust body and large, transverse punctures in the elytral striae. There are no significant differences between Australian and New Zealand specimens. The earliest New Zealand record in NZAC is an undated specimen labelled “Clevedon” by Broun (Watt 1984). The species occurs occasionally in the North Island from Northland to Wellington. Common in southeast Australia and Tasmania.

### *Proctophanes minor* (Blackburn)

Fig. 10, 37, 49, Map 7

*minor* Blackburn, 1897: 89 (*Proctammodes*); —Schmidt 1922: 364 (*Proctophanes*); —Dellacasa 1988: 162 (catalogue); —Cassis & Weir 1992: 93 (catalogue); —Stebnicka & Howden 1995: 745–746, Fig. 54, 55, 100, 123.

Length 3.2–3.8 mm, greatest width 1.5–1.8 mm. Body short oval, moderately shiny, colour piceous black, sometimes elytra lighter than fore body.

Head trapezoid with moderate median gibbosity; clypeus rounded on each side of rather deep median emargination, sides straight towards small, obtuse gena; frontal suture not visible; surface punctures fine but distinct, uniformly spaced, separated by about 1 diameter. Epipharyngeal structures as in Fig. 37.

Pronotum convex, 2× as wide as long, sides narrowly margined, basal marginal line frequently very fine, slightly crenated by punctures; median longitudinal pronotal furrow more or less distinct, closely punctate; disc with intermixed minute and large punctures, the latter separated by 1 diameter or more. Scutellum narrowly triangular, impunctate.

Elytra convex, widest at middle, humerus minutely dentate; striae deep with moderate punctures strongly crenating margins of intervals; intervals convex on disc, parallel and nearly carinate at apex, surface with minute to fine punctures.

Ventral surface shiny; metasternum more or less concave, surface punctures distinct; abdominal sternites mi-

nutely fluted along sutures, each with row of very short, pale setae; pygidium exposed, in both sexes roughly punctate, with fine longitudinal costa in basal 1/2; apical lip convex, polished.

Meso- and metafemur short with few setigerous punctures, metacoxae with 2–3 erect setae; meso- and metatibia short, apical spurs slightly curved; metatarsus as long as tibia, basal segment 1/4 shorter than upper tibial spur and shorter than following 3 tarsomeres combined.

Male. Punctures of pronotum finer and less close than in female; metasternum posteriorly with small clump of short, close setae on each side of median concavity; genitalia as in Fig. 49.

Female. Metasternum posteriorly without clump of setae; last abdominal sternite usually longer than in male.

**Type data.** Described from southeast Australia (Victoria); lectotype (BMNH) designated by Stebnicka & Howden (1995).

**Material examined.** Type specimen and 2 non-type examples; the latter placed on the same card with one specimen of *Ataenius brouni* and labelled “Plant parts - Australia, 1 Nov. 1950, Hort. Insp. Hamilton” (NZAC).

WO / –.

Nothing is known of its habits.

**Remarks.** *Proctophanes minor* has not been recorded from New Zealand before. The species is similar in size and colour to *Ataenius brouni*, but the presence of a median longitudinal impression on the pronotum and the large pronotal punctures readily separate it from *A. brouni*. The species is most closely related to *P. sculptus* and is recorded so far from Victoria and Tasmania. It is highly probable that this is an interception record, and accidental dispersal on a ship has been important in the initial spread of *P. minor* to New Zealand. There is no evidence that *P. minor* is established in New Zealand.

### Genus *Australaphodius* Balthasar

*Aphodius* (*Australaphodius*) Balthasar, 1942: 203. Type species *Aphodius melbournicus* Balthasar, by original monotypy (= *Aphodius frenchi* Blackburn).

Length 3.2–4.5 mm. Body elongate oval, glabrous above, colour black or reddish black.

Head moderately convex with slight transverse carina, clypeus emarginate medially, gena produced.

Pronotum subquadrate, base with marginal line.

Elytron with 10 striae including marginal one.

Abdomen with sternites finely fluted along sutures.



Legs moderate in length; mesocoxae slightly separate; meso- and metatibia expanded toward apex, transverse ridges developed; apical spurs of metatibia located close together below tarsal insertion.

**Remarks.** *Australaphodius* includes two African species, one of which is widely distributed. The genus is most closely related to the African genus *Harmogaster* Harold.

### *Australaphodius frenchi* (Blackburn)

Fig. 13, 38, 50, Map 8

*frenchi* Blackburn, 1892: 35 (*Aphodius*); —Schmidt 1922: 211 (*Aphodius* (*Phaeaphodius*)); —Watt 1984: 11; —Dellacasa 1988: 131 (catalogue); —Bordat 1990: 314 (*Australaphodius*); —Cassis & Weir 1992: 90 (catalogue) (*Aphodius*); —Stebnicka & Howden 1995: 763, Fig. 65, 66, 106, 125 (*Australaphodius*).

*ambiguus* Boheman, 1858: 51 (*Aphodius*) [Not *Aphodius ambiguus* Mulsant 1842: 202]; —Schmidt 1922: 211 (as a junior secondary homonym in *Aphodius*).

*melbournicus* Balthasar, 1942: 203 (*Aphodius* (*Australaphodius*)); —Bordat 1990: 314 (as synonym of *frenchi*).

Length 3.2–4.5 mm, greatest width 1.4–1.9 mm. Body shiny, reddish black to black, elytra usually lighter than head and pronotum.

Head wide, convex at middle with slight transverse carina above clypeal median emargination, surface finely punctate. Epipharyngeal structures as in Fig. 38.

Pronotum with sides and base margined, surface with punctures uniform in size, evenly spaced, usually separated by 1 diameter.

Scutellum small, triangular.

Elytra about 2.3× as long as pronotum, humeri very finely denticulate or not; striae moderately impressed and punctate; discal intervals slightly convex or flat, more convex apically. Ventral surface shiny, glabrous; mesosternum with impressed midline; abdominal sternites finely fluted along sutures and punctate on sides, penultimate sternite and pygidium with a single row of erect setae.

Legs moderate in length; mesocoxae slightly separate; transverse ridges of meso- and metatibia distinctly indicated, apical setae unequal in length; basal segment of metatarsus shorter than upper tibial spur and shorter than following three tarsomeres combined.

Male. Teminal spur of protibia bent downward, basal segment of metatarsus with apical tooth on inner side; penultimate abdominal sternite shorter than in female; genitalia as in Fig. 50.

Female. Punctures of pronotum usually closer than in male; terminal spur of protibia straight, basal segment of metatarsus without apical tooth.

**Type data.** *Aphodius frenchi*: described from South Australia, Adelaide. Lectotype and paralectotypes (SAMA) designated by Stebnicka & Howden (1995).

*Aphodius ambiguus*: described from Cape of Good Hope. Type material in NRSS.

*Aphodius melbournicus*: described from South Australia. Type material in Balthasar Collection (NMPC).

**Material examined.** Type specimens plus 10 non-type examples (NZAC).

AK, WO, HB, WI / –.

Collected April–November.

Recorded from near sea level.

Collected primarily in pitfall traps in pastures and at light in coastal forests; occasionally found under lupin bushes, at Te Maika collected under the creeping plant *Muehlenbeckia complexa* (Watt 1984).

**Remarks.** The characters of *A. frenchi*, originally described from the Cape of Good Hope under the junior homonym of *Aphodius ambiguus* seem to indicate, by their resemblance to other African species, that it is native to Africa. Currently it is widespread from Western and South Australia to Victoria, in Tasmania, and in South Africa, and is introduced in Chile (new record). Reported from New Zealand and Tasmania by Watt (1984).

## Tribe Eupariini

### Genus *Parataenius* Balthasar

*Parataenius* Balthasar, 1961: 121. Type species *Parataenius mirabilis* Balthasar, by original monotypy [= *Ataenius derbesis* (Solier, 1851)].

Length 3.5–6.0 mm. Body mostly convex, robust, glabrous above; colour rusty brown, dark brown to black.

Head moderate in size, gibbose at middle, clypeal margin obtuse or finely denticulate on each side of median emargination, surface usually transversely granulate.

Pronotum convex, sides and base margined, lateral edge finely crenate, fringed with pale setae.

Scutellum triangular.

Elytra convex, arcuate or subparallel-sided, striae impressed, punctate.

Ventral surface usually with pale setae; mesosternum and metasternum nearly equal in length; abdominal sternites coalesced, with fluting along sutures.

Legs moderate in length; meso- and metatibia relatively robust, expanded apically; apex of metatibia with fringe of short setae and more or less distinct accessory spine; apical spurs nearly equal in length, thick or slightly flattened, sinuate.

**Remarks.** The Neotropical genus *Parataenius* presently includes five species (unpublished data) distributed from the southern United States to Argentina. *Parataenius* is close to the Australian genus *Australammoecius* Petrovitz (Stebnicka & Howden 1996) and seems to occupy an intermediate position between the *Australammoecius*–*Ataenius* complex and the tribe Psammodiini.

### *Parataenius simulator* (Harold)

Fig. 11, 23, Map 9

*simulator* Harold, 1868: 85 (*Ataenius*); —Schmidt 1922: 439; —Woodruff 1973: 130, fig. 226; —Cartwright 1974: 74; —Dellacasa 1988: 281 (catalogue) (*Parataenius*); —Chalumeau 1992: 193; —Stebnicka & Howden 1996: 140–141, Fig. 85, 113.

*schwarzi* Linell, 1896: 721 (*Psammodius*); —Cartwright 1964: 103 (as synonym of *simulator*).

*granuliceps* Petrovitz, 1971: 102 (*Parataenius*); —Cassis & Weir 1992: 100 (catalogue); —Chalumeau 1992: 193 (as synonym of *simulator*).

Length 3.8–5.9 mm, greatest width 1.8–2.0 mm. Body (Fig. 11, 23) convex, shiny, colour reddish brown to black.

Head moderate in size, gibbose at middle, clypeal margin obtusely rounded or slightly angulate on each side of rather deep median emargination, then straight towards slightly protruding gena; gena noticeably fringed with setae; clypeal surface transversely wrinkled, wrinkles usually broken into tubercles; vertex punctate.

Pronotum convex, side and base margined, lateral edge finely crenate, fringed with pale setae; surface with mixed punctures, everywhere with fine, evenly distributed punctures separated by 1 diameter or more, and coarse punctures unevenly spaced, mostly in anterior and posterior angles of pronotum with some scattered across base. Scutellum triangular, impunctate.

Elytra convex, sides slightly arcuate, humeri finely denticulate; striae strongly impressed, deep striae punctures slightly crenating inner margins of intervals; intervals moderately convex with minute, scattered punctures or impunctate.

Ventral surface shiny, partially covered with pale setae; mesosternum convex, shagreened; metasternum shining, midline fine, lateral metasternal triangle elongate and deepest along anterior margin; abdominal sternites shining, finely fluted along sutures, fluting longer on successive sternites, fine to moderate punctures concentrated on sides; pygidium apically with smooth, wide lip, disc scabrously eroded with scattered long hairs.

Legs moderate in length; mesocoxae approximate; meso- and metafemur smooth, shiny, finely punctate, 3–4 coarse punctures at apex, posterior femoral lines absent; protibia broader than usual; meso- and metatibia rather

short, expanded apically; apex of metatibia with fringe of short setae, triangular accessory spine and slightly flattened spurs; basal segment of metatarsus shorter than upper tibial spur, longer than following 3 tarsal segments combined.

External sexual differences slight; usually penultimate abdominal sternite in male shorter than in female

**Type data.** *Ataenius simulator*: described from Argentina, Mendoza. Lectotype (MNHN) designated by Cartwright (1973).

*Psammodius schwarzi*: described from Florida, Jacksonville. Type material in USNM.

*Parataenius granuliceps*: described from Australia, Sydney. Type material in MHNG.

**Material examined.** Type specimens of *A. simulator* and *granuliceps* and 5 non-type examples (NZAC).

HB / –.

Collected in January at Hawkes Bay.

Occasionally found in logs and leaf litter, commonly taken at light. The New Zealand specimens are labelled as “taken in house”.

**Remarks.** *Parataenius simulator* is recognisable by its clypeal surface with transverse granules and large scattered punctures on the pronotum. It is widely distributed in the Americas, introduced in Europe (Portugal), Africa, and Australia. In America it is commonly attracted to light and seems to be rarely, if ever, a dung feeder. In Australia it has been collected in berlesates from logs and leaf litter. Jerath (1960) described the larva under the name *Ataenius schwarzi* (Linell).

### Genus *Ataenius* Harold

*Ataenius* Harold, 1867: 82, et. act. Type species *Ataenius scutellaris* Harold, by original monotypy.

Length 2.0–6.0 mm. Body variously shaped and sculptured; dorsum usually unicolorous reddish brown to black, frequently covered with setae, rarely spotted, occasionally elytra lighter than head and pronotum.

Head moderately to strongly gibbose medially, frontal suture usually marked by fine line lacking tubercles, surface variously sculptured, punctate, scabrous, transversely wrinkled, or longitudinally strigose; clypeus with anterior margin rounded, angulate, or denticulate on each side of median emargination. Eye usually well developed, not visible from directly above.

Pronotum transverse or subquadrate, usually evenly convex or with fovea and/or tumosity laterally, or with

longitudinal depression medially; sides and base margined or not, margins smooth or crenate-fimbriate, posterior angles obtuse, rounded or truncate, frequently slightly excised. Scutellum triangular, relatively small.

Elytra with basal bead, single or double humeral denticles and 10 striae and intervals including marginal one; striae variously sculptured, in some species or specimens alternate elytral intervals differing in height. Wings functional.

Ventral thoracic sclerites usually uniformly shaped; mesosternum less elevated than metasternum with fine intercoxal carina; lateral metasternal triangle distinct, rarely vague; mesocoxae contiguous or slightly separated; abdomen with 5–6 visible, coalesced sternites, sternites fluted (longitudinally strigose) along sutures or not fluted; pygidium with median transverse carina (Fig. 27), scabrous basally.

Legs moderate in length; profemur anteriorly with perimarginal groove; protibia usually with 3 teeth on outer side, rarely teeth placed otherwise; mesotibia and metatibia slightly widened toward apex, sometimes with traces of transverse ridges; apex of metatibia with or without accessory spines and with or without fringe of few setae; apical spurs thin, both located close together below tarsal insertion; tarsus short to moderate in length.

External sexual differences usually slight, apparent mostly on ventral sclerites in the length and sculpture of visible sternites, in length of tarsal segments, and (in some species) in shape of pronotum, and, rarely, in shape of terminal spur of the protibia.

Male genitalia generally homogenous in shape, moderately to strongly sclerotised; phallobase mostly without hump, equal to length of parameres or shorter; phallobase and parameres usually fused; apical portion of internal sac usually membranous, frequently furnished with sclerites and/or spicules.

**Remarks.** The above characterisation of *Ataenius* covers almost the entire world fauna. The genus now contains about 250 known species (data revised recently by the author), but by far the largest numbers of species are found in the Western Hemisphere (Neotropical and Nearctic regions) and in Australia. The New Zealand fauna includes two introduced species.

As a general rule, members of *Ataenius* are not dung feeders in either the larval and adult stages. Adults of most species are saprophagous, mostly attracted to light. Occasionally specimens can be netted flying at vegetation remnants, dung, or flowers.

### *Ataenius brouni* (Sharp)

### Broun's scarab

Fig. 12, 39, 51, Map 10

*brouni* Sharp, 1876: 71 (*Aphodius*); —Harold 1877: 92 (*Saprosites*); —Schmidt 1922: 404; —Richards 1959: 36 fig. 1; —Watt 1984: 12 fig. 13 (*Ataenius*); —Dellacasa 1988: 102 (catalogue) (*Saprosites*).

*macilentus* Blackburn, 1904: 160, 167 (*Ataenius*); —Schmidt 1922: 437; —Cassis & Weir 1992: 96 (catalogue); —Stebnicka & Howden 1997: 740, 751–753, Fig. 6, 26, 27, 97. **New synonymy.**

Length 3.0–4.0 mm, greatest width 1.3–1.9 mm. Body elongate oval, subparallel-sided, moderately shiny, usually slightly alutaceous; colour reddish black to black, anterior clypeal and pronotal margins and legs reddish, elytra frequently reddish.

Head rather wide, moderately gibbose medially; clypeal margin narrowly reflexed, rounded on each side of moderate median emargination, side arcuate or inconspicuously emarginate before obtuse, depressed gena; clypeal surface anterior to frons smooth, slightly microreticulate, impunctate, in some specimens minute punctures visible along anterior margin; frontal suture frequently indicated by weakly marked line and small convexities at eyes, vertex with band of very fine punctures separated by 1 diameter or more. Epipharyngeal structures as in Fig. 39.

Pronotum rectangular, convex; anterior angle obtusely rounded and slightly reflexed, side arcuate towards rounded posterior angle; sides and base margined by smooth, hairless line; surface more or less distinctly flattened at anterior angles with round tumosity laterally; punctures very variable in size and distribution, usually moderate, on disc separated by 1–3 diameters, closer and more uniformly spaced towards lateral margin, strongly concentrated at anterior angles, usually lacking in median anterior 1/4 of pronotum.

Elytra less convex than pronotal disc, sides slightly converging posteriorly, humeral denticle small, acute; elytral striae moderately impressed, striae punctures shallowly crenating inner margins of intervals; discal intervals usually convex, impunctate, in some specimens alutaceous.

Mesosternum finely granular, very finely pilose with well-defined carina between mesocoxae; metasternum convex, disc moderately shiny with impressed midline and few moderate punctures scattered in anterior half, lateral area and deep metasternal triangle scabrous, punctate; abdominal sternites finely fluted along anterior margins, fluting of sternite 5 longer and deeper, surface glabrous, punctures moderate in size, shallow, extending from side to side or vanishing at middle of each sternite; pygidium scabrous in apical half.

Profemur with perimarginal groove, surface narrowly shiny along groove, posterior area finely scabrous; meso- and metafemora shiny, each with 1–3 fine punctures at apex; posterior femoral lines fine, complete; meso- and metatibiae with vestiges of transverse ridges; metatibial fringe of 8–9 setae, one external seta longest; basal tarsomere of metatarsus subequal to upper tibial spur and to following three tarsomeres combined, but the latter character occurs variably in both sexes.

Male. Penultimate abdominal sternite slightly shorter than in female; genitalia as in Fig. 51.

Female. Pronotum usually narrower than in male, surface punctures denser.

**Type data.** *Ataenius browni*: Lectotype female, labelled “*Aphodius browni* Type D.S. N. Zealand.” on card, “Ex Musaeo D. Sharp 1890” (MNHN), here designated.

*Ataenius macilentus*: described from southeastern Australia (New South Wales). Lectotype (BMNH) and paralectotypes (SAMA) designated by Stebnicka & Howden (1997).

**Material examined.** Type specimens plus 273 non-type examples (AMNZ, CMNO, ISEA, LUNZ, MONZ, NZAC, OMNZ, SMTD).

ND, AK, CL, WO, TK, TO, GB, HB, WI / SD, NN, MB, KA, BR, MC, MK, SL.

Collected throughout the year.

Recorded from near sea level to about 1100 m.

The species occurs in diverse habitats; long series have been found in mixed mosses, under moss of manuka, under stones, in pastures, in pitfall traps, in a lawn, and in a house.

**Remarks.** The specimens from New Zealand differ slightly from those of Australia being relatively smaller and lighter in colour. There is some variation in the proportion of the pronotum and elytra and in the punctuation of the pronotum as mentioned in the description. The species is most closely related to *Ataenius nudus* Blackburn restricted to West Australia. Both species have a similar habitus and belong to the *A. australasiae* group of species (Stebnicka & Howden 1997).

### *Ataenius picinus* Harold

Fig. 40, 52, Map 11

*picinus* Harold, 1867: 281 (*Ataenius*); —Schmidt 1922: 422–433; —Watt 1984: 11–12; —Dellacasa 1988: 279 (catalogue); —Cassis & Weir 1992: 97 (catalogue); —Stebnicka & Howden 1997: 740, 746–748, Fig. 4, 5, 22, 99.

### pitchy scarab

*duplopunctatus* Lea, 1923: 6 (*Ataenius*); —Cartwright 1964: 103 (as synonym of *picinus*).

*boucomonti* Paulian, 1937: 41 (*Ataenius*); —Cartwright 1964: 103 (as synonym of *picinus*).

*rugosus* Richards, 1959: 41 fig. 3 (*Saprosites*); —Watt 1984: 11–12 (as synonym of *picinus*).

Length 4.8–6.0 mm, greatest width 1.8–2.5 mm. Body elongate, moderately convex, shiny; colour black, or reddish in freshly emerged specimens.

Head moderately gibbous medially, clypeal margin finely reflexed, broadly rounded on each side of moderate median emargination, sides slightly arcuate towards nearly right-angled gena; surface very finely and transversely wrinkled over anterior two-thirds, vertex with band of fine punctures. Epipharyngeal structures as in Fig. 40.

Pronotum convex, side and base strongly margined, edge finely crenate, fimbriate, crenations noticeable at anterior angle; surface with mixed punctures throughout, very fine punctures evenly spaced, separated by about twice their diameters, larger punctures slightly irregularly spaced, gradually finer and less numerous over median anterior third of disc.

Elytron with very small humeral denticle, striae deep, striae punctures crenating inner margins of moderately convex intervals; intervals with minute punctures, 9th interval finely, densely punctate.

Mesosternum shagreened, alutaceous with fine, appressed hairs, carinate between coxae; metasternum smooth, shiny, midline long and deep, surface with close, minute punctures; lateral metasternal triangle deep, smooth; abdominal sternites strongly and closely punctate from side to side, first visible sternite with posterior marginal line, following sternites fluted along anterior margin; pygidium with strong, shiny apical lip and roughly eroded disc.

Legs moderate in length; profemur with perimarginal groove, surface shiny with fine, scattered punctures and occasional coarse, crescent-shaped punctures apically; meso- and metafemora similarly punctate with strong posterior marginal line over outer half; posterior apical fringe of metatibia invariably with group of four setae and strong accessory spine; basal tarsomere of metatarsus equal in length to upper tibial spur and to following three tarsomeres combined.

Male. Penultimate abdominal sternite shorter than in female, pygidium longer with wider apex; genitalia as in Fig. 52.

Female. Pronotum slightly narrower than in male.

**Type data.** *Ataenius picinus*: described from Chile. Lectotype (MNHN) designated by Cartwright (1964).

*Ataenius duplopunctatus*: described from Australia, Parkerville. Lectotype and paralectotypes (SAMA) designated by Stebnicka & Howden (1997).

*Ataenius boucomonti*: described from Australia, Sydney. Type material in DEIE.

*Saprosites rugosus*: described from New Zealand. Holotype (sex undetermined) labelled "Holotype *Saprosites rugosus* 6/10/58 det. A.M. Richards", "Mt Roskill Auckland", "at light", "Coll. A.E. Brookes Jan. 1946" (NZAC). Paratypes (2), labelled "Auckland Museum, in house Auckland 10.Nov.1954 H. Botting", "Paratype *Saprosites rugosus* 6.x.1958 det. A.M. Richards" (AMNZ).

**Material examined.** Type specimens of *A. duplopunctatus* and *rugosus* plus 297 non-type examples (AMNZ, ANIC, ISEA, LUNZ, MONZ, NZAC).

KE / ND, AK, CL, WO, BP, GB, WI / -.

Collected throughout the year.

Recorded from near sea level.

This species is commonly collected at light, found in pitfall traps, in cow and sheep dung, leaf litter samples, soil, compost heaps, under dead marsupials and beneath stones, occasionally found in decaying banana squash, and on *Cucurbita pepo* gourds.

**Remarks.** The combination of size, the clypeal surface with transverse wrinkles and the pronotal margin broken by fringed setae identifies the common species, *A. picinus*. Ecologically very diverse, it has some potential as a minor pest; larvae were noted damaging seedlings, adults damaging strawberries, potatoes, and beans. The species is widely distributed throughout the Southern United States, Central and South America, West Indies, Fiji, New Caledonia, and Vanuatu to Australia. It was introduced to New Zealand from Australia; according to Watt (1984) Auckland was the original port of entry.

### Genus *Saprosites* Redtenbacher

*Saprosites* Redtenbacher, 1858: 436, et auctt. Type species

*Saprosites peregrinus* Redtenbacher, by original monotypy.

Length 1.0–7.0 mm. Body elongate, subparallel-sided, glabrous, shiny; dorsum always unicolorous rusty brown to black, occasionally elytra lighter than head and pronotum.

Head large, unarmed, moderately to strongly gibbose medially, rarely frontal suture marked by fine line; clypeus with anterior margin always rounded on each side of median emargination, surface simply punctate or impunctate, rarely subgranulate or granulate. Eyes usually well de-

veloped, invisible from directly above. Antenna short, usually hidden under clypeal margin.

Pronotum subquadrate, posterior angle rounded, truncate or emarginate, angulate basally or not so; base margined or without marginal line; surface with tumosity and/or fovea laterally, or with longitudinal line medially, punctures round, simple. Scutellum small, narrowly triangular.

Elytra usually flattened on disc with or without basal bead and humeral denticles; 10 striae including marginal one distinctly impressed with moderate to coarse punctures; intervals convex to flat on disc, usually convex apically. Metathoracic wings functional.

Ventral surface glabrous; prosternum usually with triangular or trapezoid process; mesosternum variously sculptured, usually convex medially with or without transverse depression in front of intercoxal carina; mesocoxae subcontiguous or separated in various degree by convex or flattened carina; metasternum convex or slightly flattened, punctate or not punctate, midline distinct; lateral metasternal triangle distinct, vague or absent; abdomen with 4–6 visible, coalesced sternites, sternites usually fluted (longitudinally strigose) along sutures; pygidium eroded basally with median longitudinal groove, exposed apical portion variously sculptured.

Legs short; profemur anteriorly often with perimarginal groove; protibia 3–dentate, frequently with minute intervening denticles and/or with two apical teeth close together; meso- and metatibiae more or less widened toward apex, sometimes with traces of transverse ridges, apices usually with accessory spines, apical spurs located close together below tarsal insertion; tarsus short to moderate in length, claws hornlike.

External sexual differences apparent mostly on ventral sclerites, in number of visible sternites and in their length, in sculpture of pygidium, in number of tibial accessory spines (in some species), in length of tarsal segments, and in shape of posterior angles of pronotum.

Male genitalia generally homogeneous in shape, moderately sclerotised (Fig. 53–59). Phallobase without dorsal hump, equal to length of parameres or shorter; phallobase and parameres usually fused; apical portion of internal sac membranous, usually large, baggy, furnished with sclerites and/or spicules.

**Remarks.** The above diagnosis covers almost the entire world fauna of *Saprosites sensu stricto*. The genus includes approximately 130 species distributed mostly in Indomalaya, Indonesia, Australia, Madagascar, South Africa, and Central and South America. The species are attracted to light, live in moss, leaf litter, and in the dead,

rotten trunks of many tree species. The genus is in need of a careful revision on a worldwide basis. Most of the specific descriptions hitherto given relate to the superficial, secondary characters which are often sex dependent or too plastic to be useful.

Eight of the nine species of *Saprosites* occurring in New Zealand are restricted to New Zealand. Three species, *Saprosites exsculptus* (White), *S. distans* (Sharp), and *S. raoulensis* (Broun), share similar combinations of the character states with neotropical species, such as *S. dentipes* Harold, *S. sulcatus* Harold, and *S. medians* Harold (Stebnicka 2001, in press). The remaining four species are apparently closely related to the Australian species such as *S. nitidicollis* (Macleay) and *S. sternalis* (Blackburn) (Stebnicka & Howden 1996).

### *Saprosites mendax* (Blackburn)

Fig. 14, 32, Map 12

*mendax* Blackburn, 1892: 36 (*Ataenius*); —Blackburn 1904: 176 (*Saprosites*); —Schmidt 1922: 412; —Watt 1984: 12, fig. 12; —Dellacasa 1988: 161 (catalogue); —Cassis & Weir 1992: 100 (catalogue); —Stebnicka & Howden 1996: 163, 165–166. *punctatus* Richards, 1959: 45, fig. 6: 1–5; —Watt 1984: 12 (as synonym of *mendax*).

Length 3.2–3.5 mm, greatest width 1.0–1.2 mm. Colour black; castaneous or rusty brown in freshly emerged specimens.

Head large, convex, clypeal margin widely rounded on each side of moderate median emargination, gena more or less protruding; surface alutaceous anteriorly with fine but deep, evenly spaced punctures separated by 1 diameter. Epipharyngeal structures similar to *communis-watti* (Fig. 42–43).

Pronotum moderately convex, side margins visible from directly above; anterior angle reflexed, posterior angle more or less excised before prominent basal angulation; sides and base strongly margined, marginal line grooved and crenate; surface punctures mixed, fine and large, fine punctures concentrated at anterior margin and laterally to posterior angles of pronotum, large punctures variable in size and density, usually separated by 1–2 times their diameter on disc, strongly concentrated within fovea.

Elytra parallel-sided or slightly arcuate, humerus strongly and sharply denticulate; striae impressed with moderate to coarse punctures crenating margins of intervals; discal intervals convex, more convex apically, minutely punctate or not so.

Ventral surface glabrous; mesosternum (Fig. 32) flattened longitudinally at middle or slightly convex, more or less distinctly longitudinally punctate, rarely with very slight transverse depression in front of intercoxal carina; intercoxal space nearly equal to width of mesofemur;

metasternum convex, midline strongly impressed; surface finely punctate on disc and part way to metacoxae; lateral metasternal triangle absent or indicated by group of fine punctures; abdomen with six visible sternites; each sternite coarsely fluted in anterior 1/3 and irregularly concave on sides, pygidium finely punctate.

Legs short; profemur without perimarginal groove, slightly wider than mesofemur, all femora shiny; meso- and metatibiae as long as femora; apex of metatibia with 2 accessory spines and arcuate spurs; tarsus as long as tibia.

Male. Penultimate abdominal sternite nearly as long as preceding one; exposed portion of pygidium longer than eroded base; upper tibial spur equal in length to first two tarsomeres combined; genitalia similar to *kingsensis-watti-communis* (Fig. 55, 56, 58).

Female. Penultimate abdominal sternite 1/3 longer than preceding one; exposed portion of pygidium shorter than eroded base; upper tibial spur longer than first two tarsomeres combined.

**Type data.** *Saprosites mendax*: Type not seen, probably in BMNH. Syntypes (5). 1, with handwritten 'H.245' on card, labelled 'Victoria', '*Ataenius mendax* Cotype'; 4, labelled 'For.R.' on card, 'N. S. Wales', '*mendax* Blackb.' (SAMA).

*Saprosites punctatus*: Holotype male, labelled "Holotype *Saprosites punctatus* 6/10/58 det. A.M. Richards", "ex decaying apple tree Remuera Auckland 20 Aug. 1950 K.P. Lamb", "C.I.E. Coll. No 58/9" (NZAC). Paratypes (5), same data as holotype (NZAC).

**Material examined.** Type specimens plus 52 non-type examples (AMNZ, CMNO, LUNZ, NZAC).

AK / –.

Collected throughout the year.

Recorded primarily from near sea level.

Found in variety of habits in urban areas, such as soil, decayed wood, lawn compost, garden leaf litter, carrion, under bark, and in pitfall traps. Common at Lynfield (AK), and occasionally found in *Acacia* paddock, under bark of apple trees, and *Eucalyptus* ("bluegum").

**Remarks.** *Saprosites mendax* is distinguished by the combination of its size, and the pronotal posterior angles excised before the basal angulation. There are no significant differences between New Zealand and Australian specimens. The species is limited in distribution to the southeastern area of Australia including Tasmania and to the Auckland urban area of New Zealand. Introduced to England (new record). In Australia this species is found

under bark of *Eucalyptus regnans*, *Nothofagus cunninghami*, and *Acacia* sp., in log litter, and fungi in *Eugenia* temperate rainforest, on sandy beaches, in soil, and at light.

### *Saprosites exsculptus* (White)

Fig. 15, 53, Map 13

*exsculptus* White, 1846: 9 (*Oxyomus*); —Harold 1861: 111 (*Proctophanes*); —Harold 1877: 92 (*Saprosites*); —Broun 1880: 258 (*Aphodius*) (misidentification); —Schmidt 1922: 407–408 (*Saprosites*); —Richards 1959: 38–40, fig. 2: 1–5; —Dellacasa 1988: 136 (catalogue).

*Pascoe* Sharp, 1876: 71 (*Aphodius*); —Schmidt 1908: 119 (*Saprosites*); —1922: 413; —Richards 1959: 38 (as synonym of *exsculptus*); —Dellacasa 1988: 292 (catalogue) [as synonym of *communis* (sic!)].

*suspectus* Sharp, 1876: 70 (*Aphodius*); —Harold 1877: 92 (*Saprosites*); —Schmidt 1922: 413; —Richards 1959: 38 (as synonym of *exsculptus*); —Dellacasa 1988: 293 (catalogue) (as synonym of *exsculptus*).

Length 5.2–5.5 mm, greatest width 1.9–2.0 mm. Body robust, elongate, shiny black or rusty brown in freshly emerged specimens; clypeal and pronotal margins usually reddish.

Head large, gibbose at middle; clypeal margin narrowly upturned, rounded on each side of moderate median emargination, side slightly arcuate or straight towards right-angled, very prominent gena; clypeal surface transversely concave just above median emargination, punctures fine, evenly spaced, gradually increasing in size from median area to vertex, separated by 1 diameter. Epipharyngeal structures similar to those in *S. distans* (Fig. 41).

Pronotum subquadrate, convex, widest at middle; anterior angle rounded, side arcuate towards sharp, prominent angulation of posterior angle; lateral margin grooved, slightly upturned and crenate in posterior half, base with row of coarse, close punctures, sometimes with trace of marginal line; pronotal surface flattened at anterior angles, lateral tumosity distinct, punctures mixed, minute and large, the latter irregularly spaced, variable in density, on disc separated by about 1–3 diameters, largest strongly concentrated at anterior angle, vanishing along anterior margin. Scutellum narrow, triangular, impunctate.

Elytra parallel-sided, elongate, humerus with large, obtuse epipleural denticle; striae deep with coarse punctures strongly crenating inner margins of intervals; intervals convex, shiny, impunctate or with few minute, scattered punctures; 9th intervals shorter than remaining ones.

Ventral surface slightly alutaceous; prosternal process triangular with clump of long yellow hairs; mesosternum with impunctate area medially, fine punctures on sides,

meso-metasternal carina flattened; space between metacoxae significantly smaller than width of mesofemur; metasternum convex, longer than mesosternum, midline impressed, punctures very fine, variable in density, lateral metasternal triangle absent; abdominal sternites coalesced, grooved and fluted along sutures, surface of sternite 2 slightly longitudinally strigose; exposed portion of pygidium smooth.

Legs relatively short; all femora smooth, impunctate or with minute scattered punctures; protibia 3–dentate without intervening denticles; meso- and metatibiae as long as femora, expanded apically; apex of metatibia with two strong accessory spines including external one, apical spurs slender, unequal in length, bottom spur short; metatarsus shorter than tibia, basal tarsomere shorter than upper tibial spur and shorter than following three tarsomeres combined.

Male. Penultimate abdominal sternite less arcuate ventrally and shorter than in female, fluting along sternites coarser, especially on sides; genitalia as in Fig. 53.

Female. Punctures of pronotum usually slightly larger than in male; exposed portion of pygidium shorter than eroded base.

**Type data.** *Oxyomus exsculptus*: Lectotype (sex undetermined) labelled “Type”, “Port Nicholson”, “*Oxyomus exsculptus* White” (BMNH), here designated.

*Aphodius Pascoe*: Lectotype male, labelled “*Aphodius Pascoe* Type D.S. N. Zeald. on card, “Ex Musaeo D. Sharp 1890” (MNHN), here designated.

*Aphodius suspectus*: Lectotype female, labelled “*Aphodius suspectus* Type D.S. N. Zeald.” on card, “Ex Musaeo D. Sharp 1890” (MNHN), here designated.

**Material examined.** Type specimens plus 104 non-type examples (AMNZ, CMNO, CMNZ, ISEA, LUNZ, MONZ, NZAC, OMNZ, SMTD).

ND, AK, CL, WN, WA / –.

Collected January–April and August–November.

Recorded from sea level to 700 m.

Found beneath stones, under bark, and in rotten wood. At Te Henga (AK) collected under dead *Corynocarpus laevigatus*, at Kakatarahoe (CL) beaten from flowering shrubs. Most probably diurnally active.

**Remarks.** This species is most closely related to *S. distans* (see Remarks under that species) and is often misidentified in collections. It is readily distinguished from *S. distans* in having a more robust body, the head with distinct punctures, the metatibia furnished with a strong accessory spines, the elytra with larger, obtuse humeral denticles

and larger punctures in the striae. In general body shape it is close to the South American species of the genus, mostly to *S. dentipes* Harold. Indigenous to New Zealand, found, up to now, exclusively in the North Island.

### ***Saprosites distans* (Sharp)**

Fig. 16, 41, 54, Map 14

*distans* Sharp, 1876: 70 (*Aphodius*); —Harold 1877: 92 (*Saprosites*); —Broun 1880: 258 (*Aphodius*) (as synonym of *exsculptus*); —Schmidt 1922: 407–408 (*Saprosites*) (as synonym of *exsculptus*); —Richards 1959: 40; —Dellacasa 1988: 288 (catalogue).

*candens* Broun, 1880: 258–259 (*Aphodius*); —Schmidt 1908: 117 (*Saprosites*); —1922: 409; —Richards 1959: 40–41; —Dellacasa 1988: 104 catalogue). **New synonymy.**

Length 4.7–5.1 mm, greatest width 1.5–1.8 mm. Body elongate, slender, moderately shiny, black or reddish black; clypeal and pronotal margins and legs reddish.

Head large, gibbose at middle, clypeal margin narrowly upturned, rounded on each side of moderate median emargination, side straight or inconspicuously emarginate before right-angled, distinctly prominent gena; surface alutaceous, transversely concave just above median emargination, vertex with minute to very fine punctures separated by more than 1 diameter. Epipharyngeal structures as in Fig. 41.

Pronotum rectangular, moderately convex, widest in anterior half; anterior angle obtusely rounded, side rounded towards sharp angulation of posterior angle; lateral margin weakly grooved and upturned, smooth, sometimes with very slight crenations near posterior angulation; base with distinct marginal line, in some specimens line narrowly broken at middle of base; surface flattened at anterior angles, lateral tumosity weak, punctures mixed, minute and large, the latter slightly increasing in size from anterior half to base of pronotum, irregularly spaced, variable in density, on disc separated by 1–3 diameters, strongly concentrated at anterior angles. Scutellum narrow, triangular, impunctate.

Elytra elongate, slightly widened in apical third; humerus with conical, sharply pointed epipleural denticle; striae deep with moderate punctures crenating inner margins of intervals; discal intervals usually flat, becoming moderately convex toward apices, surface impunctate, sometimes slightly alutaceous; 9th interval shorter than the remaining ones.

Ventral surface slightly alutaceous; prosternal process tuberculate, not prominent, without hairs; mesosternum punctate on each side of flattened meso-metasternal carina; space between mesocoxae nearly equal to width of mesofemur; metasternum convex, longer than mesoster-

num, midline impressed, punctures fine, variable in density, metasternal triangle absent; abdominal sternites coalesced, grooved and finely fluted along sutures, surface impunctate; exposed portion of pygidium smooth.

Legs relatively long; all femora smooth or with minute scattered punctures; protibia 3-dentate without intervening denticles; meso- and metatibiae as long as femora, weakly expanded apically; apex of metatibia with two small accessory spines including external one, apical spurs slender, unequal in length; metatarsus as long as tibia, basal tarsomere equal in length to upper tibial spur and subequal to following three tarsomeres combined.

Male. Pronotum usually shorter than in female, penultimate abdominal sternite less arcuate, and shorter at middle; genitalia as in Fig. 54.

Female. Punctures of pronotum usually closer and somewhat larger than in male; exposed portion of pygidium shorter than eroded base.

**Type data.** *Aphodius distans*: Lectotype male, labelled “*Aphodius distans* Type D.S. N. Zealand.” on card, “Ex Musaeo D. Sharp 1890” (MNHN), here designated.

Paralectotype, labelled “Typus”, “Greymouth New Zealand”, “*Aphodius distans* mihi D.S.”, “coll. R. Petrovitz” (MHNG).

*Aphodius candens*: Lectotype (sex undetermined) labelled “Type”, “*Aphodius candens*” “New Zealand Broun Coll. Brit. Mus. 1922–482” (BMNH), here designated.

**Material examined.** Type specimens plus 26 non-type examples (CMNZ, ISEA, LUNZ, NZAC, OMNZ, SMTD).

CL, BP, TK, GB, RI, HB / NN, BR.

Collected January to April, in July and November.

Recorded from sea level to near 1800 m.

Found primarily at night near water, in rotten logs on sand and beneath stones. At Raetihi (RI) collected on *Nothofagus*. Most probably nocturnally active.

**Remarks.** *Saprosites distans* is quite distinct in having the shape of the hind legs similar to that of *Ataenius* rather than of *Saprosites*. The latter character shows evidence of homoplasy. The species is undoubtedly most closely related to *S. exsculptus* (see Remarks under that species) in the form of the head, pronotum, and elytra, and the male genitalia (Fig. 53, 54). The species is indigenous to New Zealand, and in the North Island is partially sympatric with *S. exsculptus*.



***Saprosites raoulensis* (Broun)**

Fig. 17, Map 15

*raoulensis* Broun, 1910: 295 (*Aphodius*); —Schmidt 1922: 329 (*Saprosites*); —Richards 1959: 48–49, fig. 8: 1–5 ; —Dellacasa 1988 : 292 (catalogue).

Length 4.7–4.8 mm, greatest width 1.6–1.8 mm. Body robust, elongate, shiny black, clypeal and pronotal margins reddish.

Head large, gibbose at middle; clypeal margin narrowly reflexed, rounded on each side of moderate median emargination, side straight towards right-angled, prominent gena; clypeal surface transversely concave just above median emargination, punctures fine, evenly spaced, gradually increasing in size from median area to vertex, separated by 1 diameter.

Pronotum subquadrate, convex, widest at middle; anterior angle rounded, side arcuate towards sharply angulate posterior angle; lateral margin weakly grooved, slightly upturned and crenate in posterior half, base with row of coarse, close punctures, without marginal line; pronotal surface flattened at anterior angles, lateral tumosity feebly marked, punctures mixed, minute and large, latter irregularly spaced, on disc separated by about 1–3 diameters, largest concentrated at anterior angles, vanishing along anterior margin. Scutellum narrow, triangular, impunctate.

Elytra parallel-sided, elongate, humerus with moderate sized, obtuse epipleural denticle; striae deep with coarse punctures strongly crenating inner margins of intervals; intervals convex about 1.5 times as wide as striae, shiny impunctate or with few minute, scattered punctures.

Ventral surface slightly alutaceous; prosternal process triangular with clump of long yellow hairs; mesosternum with impunctate area medially, fine punctures on sides, meso-metasternal carina flattened; space between metacoxae smaller than width of mesofemur; metasternum convex, longer than mesosternum, midline impressed, punctures very fine, variable in density, lateral metasternal triangle absent; abdominal sternites coalesced, grooved, and fluted along sutures; exposed portion of pygidium smooth.

Legs relatively short; all femora smooth, impunctate or with minute scattered punctures; protibia 3–dentate without intervening denticles; meso- and metatibiae as long as femora, expanded apically; apex of metatibia with two accessory spines including external one, apical spurs slender, unequal in length, bottom spur short; metatarsus shorter than tibia, basal tarsomere shorter than upper tibial spur and shorter than following three tarsomeres combined.

Male. Penultimate abdominal sternite less arcuate ventrally and shorter than in female, fluting along sterni-

tes coarser, especially on sides; genitalia similar to those in *S. exsculptus* (Fig. 53).

Female. Punctures of pronotum slightly larger than in male.

**Type data.** Holotype (sex undetermined), labelled “Raoul (Sunday) Island. coll. Mr. Wallace” (AMNZ).

Paratypes (2) labelled “Sunday Is. Kermadec Is. Exped. 1908”, “*Aphodius raoulensis* Broun”, “Ent. Div. D.S.I.R. New Zealand”, “*Saprosites raoulensis* (Broun) det. Cartw. 74” (NZAC).

**Material examined.** Paratypes and 2 non-type examples (MHNG).

KE / - / -.

Nothing seems to be recorded of its habits.

**Remarks.** *Saprosites raoulensis* is generally similar in appearance to *S. exsculptus* but is smaller, the humeral denticles of the elytra are smaller, the legs are more slender and the accessory spines of the metatibia are significantly smaller. Endemic to Kermadec Islands.

***Saprosites communis* (Broun)**

Fig. 18, 42, 55, Map 16

*communis* Broun, 1880: 260 (*Aphodius*); —Schmidt 1922: 404 (*Saprosites*); —Richards 1959: 42–43, fig. 4: 1–5 ; —Dellacasa 1988: 112 (catalogue).

Length 3.0–3.5 mm, greatest width 1.0–1.1 mm. Body parallel-sided, shiny, colour reddish black to black; proportions of body variable.

Head nearly as wide as pronotum, median gibbosity moderate; clypeal margin rounded on each side of shallow median emargination, side straight towards right-angled, prominent gena; clypeal surface slightly transversely concave just above median emargination, punctures fine, usually distinct, evenly spaced from anterior margin over median convexity, slightly larger on vertex, separated by about 1 diameter. Epipharyngeal structures as in Fig. 42.

Pronotum subquadrate, moderately convex, widest at middle; anterior angle obtuse, posterior angle broadly rounded to base and distinctly crenate-serrate, base with fine but distinct marginal line; surface flattened at anterior angles, lateral tumosity indicated, punctures mixed, fine and coarse, fine punctures same size as those on vertex, evenly distributed, more or less clearly visible along anterior margin, separated by 1 diameter; large punctures uneven, variable in density, on disc usually forming me-

dian longitudinal line, strongly concentrated on sides and at anterior angles, scattered along base and absent on lateral tumosity and along anterior margin of pronotum. Scutellum small, triangular, impunctate.

Elytron usually about 2.5 times as long as pronotum; humeral denticle conical, sharply pointed and protruding laterally; striae deep with nearly contiguous punctures crenating inner margins of intervals; intervals convex, impunctate, 7th and 9th intervals united at apical 2/3 of elytra, 8th interval shorter than the remaining ones.

Ventral surface slightly alutaceous; mesosternum strongly convex in anterior half, impunctate, with slight transverse depression in front of intercoxal, flattened carina; intercoxal space significantly smaller than width of mesofemur; metasternum convex, midline strongly impressed, surface finely punctate, lateral metasternal triangle absent; abdominal sternites coarsely fluted along sutures, especially on sides; exposed portion of pygidium shiny, finely punctate.

Femora smooth, impunctate or with few minute scattered punctures; meso- and metatibiae as long as femora; apex of metatibia with only external, fine spine, spurs thin; tarsus nearly as long as tibia, basal tarsomere shorter than upper tibial spur and shorter than three following tarsomeres combined.

Male. Penultimate abdominal sternite shorter and less arcuate ventrally than in female; genitalia as in Fig. 55.

Female. Pronotal punctures usually larger than in male, marginal crenation finer; fluting of abdominal sternites less coarse, exposed portion of pygidium shorter.

**Type data.** Lectotype (sex undetermined) labelled "Type", "Mt Arth[ur]", "*Aphodius communis*", "New Zealand Broun Coll. Brit. Mus. 1922-482" (BMNH), here designated.

Paralectotype, labelled "458", "T. Broun Collection", "A.E. Brookes Collection", "Syntype *Aphodius communis* Broun 1880" (NZAC).

**Material examined.** Type specimens plus 280 non-type examples (AMNZ, CMNO, CMNZ, ISEA, LUNZ, MONZ, NZAC, SMNS, SMTD).

ND, AK, CL, WO, BP, TK, TO, GB, RI, WN, WA / SD, NN, MB, KA, BR, WD, MC, SC, OL, FD, SL, SI.

Collected throughout the year.

Recorded from sea level to near 1800 m.

Found in a great variety of habitats such as leaf litter, decaying wood and ferns, under bark, stones and rocks, on fungi, and in moss. Occasionally found in moss under manuka, in litter of *Melicytus*, *Olearia*, *Fuchsia* and in beech forests, in rotten logs of *Pinus radiata*, *Hebe*

*elliptica*, *Sophora microphylla*, and *Nothofagus*. One fossil specimen (NZAC) was found at Waiotahi V., Ohiwa Harb. (BP) Feb. 1982, in carbonised archaeological site N 78/346.

**Remarks.** As might be expected, demes of this widespread species vary considerably. Some specimens have the pronotal median line distinctly indicated and the punctures more pronounced, in some specimens these characters are not clearly visible. *Saprosites communis* is closest to *S. kingsensis* sp.n. (see Remarks under that species) but may be distinguished by the characters given in the key. Indigenous to New Zealand, it is the commonest and most widely distributed species of *Saprosites*.

### *Saprosites kingsensis* new species

Fig. 19, 56, Map 17

Length 3.0–3.4 mm, greatest width 1.0–1.1 mm. Body parallel-sided, shiny, colour reddish black to black.

Head nearly as wide as pronotum, median gibbosity moderate; clypeal margin rounded on each side of shallow median emargination, sides straight towards right-angled, prominent gena; clypeal surface slightly transversely concave just above median emargination, punctures of anterior median area minute and indistinct, slightly larger on vertex, scattered. Epipharyngeal structures similar to *communis* (Fig. 42).

Pronotum subquadrate, moderately convex, widest at middle; anterior angle obtuse, posterior angle broadly rounded to base, minutely crenate or crenations not visible, base with fine marginal line; surface flattened at anterior angles, lateral tumosity indicated, median longitudinal line lacking; punctures mixed fine and large, fine punctures same size as those on vertex, evenly distributed, visible along anterior margin, separated by 1 diameter, large punctures unevenly spaced, strongly concentrated on sides and at anterior angles, scattered along base and absent on lateral tumosity and along anterior margin of pronotum. Scutellum small, triangular, impunctate.

Elytron relatively short, usually about 2 times as long as pronotum; humeral denticle conical, sharply pointed and protruding laterally; striae deep with nearly contiguous punctures crenating inner margins of intervals; intervals convex, impunctate, 7th and 9th intervals united at apical 2/3 of elytra, 8th intervals shorter than the remaining ones.

Ventral surface slightly alutaceous; mesosternum strongly convex in anterior half, impunctate, with slight transverse depression in front of intercoxal, flattened ca-

rina; intercoxal space significantly smaller than width of mesofemur; metasternum convex, midline strongly impressed, surface finely punctate, lateral metasternal triangle absent; abdominal sternites with fine to moderate fluting along sutures; exposed portion of pygidium shiny, finely punctate.

Femora smooth, impunctate or with few minute, scattered punctures; meso- and metatibiae as long as femora; apex of metatibia with only external, fine spine, spurs thin; tarsus nearly as long as tibia, basal tarsomere shorter than upper tibial spur and shorter than three following tarsomeres combined.

Male. Penultimate abdominal sternite shorter and less arcuate than in female; genitalia Fig. 56.

**Type data.** Holotype: male, Three Kings Islands, Great I., Castaway Camp, Nov. 1970, NZ Ent. Div. Exp. G. Kuschel (NZAC).

Paratypes: (17; ISEA, NZAC). Three Kings Is. Great I., Castaway Camp, NZ Ent. Div. Exp. Nov. 1970, Kuschel (12); Tasman Valley, Watt (2); 6 Oct. 1948, Turbott (3).

**Material examined.** Type series only (ISEA, NZAC).

TH / - / -.

Collected October, November.

Recorded from sea level.

Found in leaf mould, in litter, and under moss.

**Remarks.** *Saprosites kingsensis* is closest to *S. communis* in its large elytral denticles and in the similar form of the head and pronotum. It is distinguished by the lack of median line and marginal crenation on the pronotum, by smaller pronotal punctures and shorter elytra. It seems to be restricted to the Three Kings Islands.

### *Saprosites fortipes* (Broun)

Fig. 20, 24, 57, Map 18

*fortipes* Broun, 1881: 954–955 (*Aphodius*); —Schmidt 1922: 329 (*Saprosites*); —Richards 1959: 44–45, fig. 5: 1–5; —Dellacasa 1988: 131 (catalogue).

Length 2.5–3.3 mm, greatest width 1.1–1.2 mm. Body elongate oval, shiny, reddish black to black, or rusty brown in freshly emerged specimens.

Head as wide as pronotum, gibbose medially; clypeal margin broadly rounded on each side of narrow median emargination, sides slightly arcuate towards right-angled and slightly prominent gena; clypeal surface feebly concave just above median emargination, anterior median area with minute, scarcely visible punctures becoming more

clearly visible on vertex, separated by 1–3 diameters. Epipharyngeal structures similar to those of *S. kingsensis* (Fig. 43).

Pronotum convex; anterior angles obtuse, side rounded toward base, basal margin with row of punctures, lacking marginal line; pronotal surface flattened at anterior angles with distinct tumosity laterally, punctures mixed, very minute to fine and moderate, in some specimens minute punctures scarcely visible or visible only along anterior margin; larger punctures unevenly spaced, variable in size and density, usually scattered on disc, separated by 1–4 diameters, becoming closer on sides to anterior angles but not strongly concentrated, absent along anterior margin and on lateral tumosity. Scutellum small, triangular, impunctate.

Elytron about 2.3 times as long as pronotum, slightly arcuate toward apex or not arcuate; humeral denticle moderate in size, acute; striae deep with round, more or less close punctures slightly crenating inner margins of intervals; intervals gradually widened toward apex, convex, impunctate; 7th and 9th intervals united at half of elytral length, 8th interval very short, markedly shorter than the remaining ones.

Ventral surface shiny; mesosternum convex, smooth at middle, finely punctate laterally without visible depression in front of intercoxal carina; space between mesocoxae a little smaller than width of mesofemur, intercoxal carina narrow, convex; metasternum convex, midline weakly indicated, sometimes shallowly foveate posteriorly, surface impunctate, lateral metasternal triangle absent; abdominal sternites grooved and very finely fluted along sutures, surface smooth; exposed portion of pygidium shiny, minutely punctate.

Legs relatively short; all femora smooth, impunctate; meso- and metatibiae as long as femora; mesotibia usually wider at apex than metatibia; apex of metatibia without accessory spines, spurs slender, unequal in length; tarsus shorter than tibia, basal tarsomere shorter than upper tibial spur and shorter than following three tarsomeres combined.

Male. Penultimate abdominal sternite shorter and less arcuate ventrally than in female; genitalia as in Fig. 57.

Female. Punctures of pronotum usually closer than in male; exposed portion of pygidium shorter than eroded base.

**Type data.** Lectotype (sex undetermined), the anterior specimen of two on card, and paralectotype the posterior specimen, labelled “Type”, “*Aphodius fortipes*”, “New Zeal. Broun Coll. Brit. Mus. 1922–482” (BMNH), here designated.

**Material examined.** Type specimens plus 43 non type examples (AMNZ, ISEA, LUNZ, MONZ, NZAC).

ND, AK, CL / NN, MB, BR, DN, SL.

Collected October to June.

Recorded from coastal areas.

Found under logs, in leaf litter of coastal forests, and in pitfall traps.

**Remarks.** *Saprosites fortipes* is readily recognised by having a characteristic, very short 8th elytral interval, and intervals 7 and 9 united at the midpoint of the elytral length. Uncommon in collections, it was unrecognised by Richards (1959) and labelled as *S. communis*.

### *Saprosites watti* new species

Fig. 21, 43, 58, Map 19

Length 2.5–3.2 mm, greatest width 1.1–1.2 mm. Body elongate oval, shiny, reddish black or black, elytra usually lighter than head and pronotum.

Head subquadrate, strongly gibbose medially; clypeal margin broadly rounded on each side of narrow median emargination, sides slightly arcuate towards very small, weakly prominent gena; clypeal surface feebly concave just above median emargination, anterior median area slightly alutaceous with minute punctures becoming more clearly visible on sides and on vertex, separated by 1–3 diameters. Epipharyngeal structures as in Fig. 43

Pronotum convex; anterior angle obtuse, side arcuately rounded toward base, lateral edge and base with distinct marginal line, margins smooth, sometimes basal line finely crenated by punctures; pronotal surface flattened at anterior angles with distinct tomosity laterally, punctures mixed, very minute and moderate to large; minute punctures same size as those of head, in some specimens vanishing or visible only along anterior margin; larger punctures unevenly spaced, variable in size and density, usually scattered on disc, becoming nearly contiguous toward sides and at anterior angles, absent along anterior margin. Scutellum small, triangular, impunctate.

Elytron about 2.3 times as long as pronotum, slightly arcuate toward apex, humeral denticle very small, acute; striae deep with large punctures nearly same size as those of pronotum, punctures round, not quite contiguous, deepest at base of elytra, distinctly crenating inner margins of intervals; intervals convex, shining, impunctate; 7th and 9th intervals united in apical 2/3 of elytra, intervals 5, 6, 8, 9 equal in length, shorter than the remaining ones.

Ventral surface shiny; mesosternum convex, smooth at middle, finely punctate laterally with distinct transverse depression in front of intercoxal carina; space between mesocoxae equal to width of mesofemur, intercoxal

carina narrow, convex; metasternum convex, midline weakly indicated, sometimes shallowly foveate posteriorly, surface impunctate, lateral metasternal triangle absent; abdominal sternites grooved and very finely fluted along sutures, surface smooth; exposed portion of pygidium shiny, minutely punctate.

Legs relatively short; all femora smooth, impunctate; meso- and metatibiae as long as femora; apex of metatibia without accessory spines, spurs slender, unequal in length; tarsus shorter than tibia, basal tarsomere subequal in length to upper tibial spur and shorter than following three tarsomeres combined.

Male. Penultimate abdominal sternite shorter and less arcuate ventrally than in female; genitalia as in Fig. 58.

Female. Elytra usually slightly longer than in male; exposed portion of pygidium shorter than eroded base.

**Type data.** Holotype: male, [WD] Pleasant Flat Bridge, Haast River, 75 m, 25 May 1965, D.J. Kershaw (NZAC).

Paratypes: (118); AMNZ, CMNO, ISEA, LUNZ, NZAC). **South Island.** NN. Farewell Spit, 10 May 1967 and 27 Oct 1965, Alack & Simpson (14). **MB.** Schroders Ck, 2600 ft, [790 m] Upper Wairau Valley, 5,9 Sep 1966, L.P. Marchant & J.I. Townsend (6). **BR.** Lake Rotoiti, 23 Feb 1963, G. Kuschel (1). Inangahua, 23 Jan 1957, E.S. Gourlay (14). Cannibal Gorge, Upper Maruia River, 17 Feb 1962, Sinclair (1). Little Totara R., Charleston, 18 Jan 1969, J.I. Townsend (1). **WD.** Pleasant Flat Bridge, Haast River, 75 m, 25 May 1965, D.J. Kershaw (30). Hokitika, Glow Worm Dell, 28 Jan 1978, S. Peck (7). Waitaha River, W coast, 27 Oct 1966, J.I. Townsend (1). Greenstone Ck, Haast Pass Rd, 7 Dec 1966, A.K. Walker (1). Okuru, Jacksons Bay, 6 Dec. 1966, Walker (1). Upper Callery Gor. Tr. Westland, 2 Dec 1965, J.I. Townsend (3). Paddy's Lookout, State Highway 73, Feb–Jul 1971 and 19 Sep 1976, R.M. Emberson (11). **MC.** Mt Algidus (no other data) (1). **FD.** Lake Manapouri, W Arm, 22 Feb 1965, A.K. Walker (14). Lake Manapouri, W Arm, Mouth of Spey River, 22 Feb 1965, A.K. Walker (3). Lake Manapouri, Hope Arm, 7 Jan 1923, A.E. Brooks (7). Lake Manapouri (no other data) (2).

**Material examined.** Type series only.

– / NN, MB, BR, WD, SC, FD.

Collected January, February, May, September, October, December.

Recorded from near sea level to about 800 m.

Commonly found in moss and in leaf litter under beech trees, under *Nothofagus solandri* at Wairau Valley (MB), and in tree fern litter (*Cyathea medullaris*) in Westland.

**Remarks.** *Saprosites watti* is quite distinct by having a very small gena, the sides of the elytra slightly arcuate,

the elytral striae with round punctures being slightly separate from each other. It is certainly close to *S. fortipes* in the form of the pronotum and elytra, and to *S. sulcatissimus* in the shape of the head. The species seems to be restricted to the South Island. Unrecognised by Richards (1959), some specimens have been labelled as *S. communis*.

**Etymology.** Named for J.C. Watt who first recognised this species as new.

### *Saprosites sulcatissimus* (Broun)

Fig. 22, 25, 59, Map 20

*sulcatissimus* Broun, 1911: 101 (*Aphodius*); —Schmidt 1922: 329 (*Saprosites*); —Richards 1959: 46–48, fig. 7: 1–5; —Dellacasa 1988: 293 (catalogue).

Length 3.5–3.8 mm, greatest width 1.3–1.4 mm. Body elongate oval, shiny, colour carbon black to black, clypeal margin and legs reddish, in some specimens elytra slightly lighter than head and pronotum; proportions of body variable.

Head subquadrate, strongly gibbose medially; clypeal margin broadly rounded on each side of narrow median emargination, sides slightly arcuate towards small, slightly prominent gena; surface feebly concave just above median emargination, anterior median area with very fine, close punctures, sometimes with minute lines of 2–3 united punctures, median area with minute punctures becoming more clearly visible on vertex, separated by 1 diameter. Epipharyngeal structures similar to those in *S. kingsensis* (Fig. 43).

Pronotum convex; anterior angles obtuse, side arcuately rounded towards base, lateral edge with distinct, smooth, grooved marginal line, basal marginal line finer but distinct; pronotal surface flattened at anterior angles with tumosity laterally, punctures mixed, minute to fine and large, fine punctures evenly spaced, more or less clearly visible in anterior 1/3 of pronotum, larger punctures unevenly distributed, variable in density, usually strongly concentrated at middle of disc, separated by 1 diameter or less, in some specimens forming median longitudinal line, absent along anterior and lateral margins. Scutellum small, triangular, impunctate.

Elytra about 2.3 times as long as pronotum, parallel-sided; humeral denticle conical, large and acute; striae very deep, wide, slightly elongate punctures located within striae and slightly crenate inner margins of intervals; intervals subcarinate, nearly as wide as striae, shining, impunctate; 7th and 9th intervals united at apical 2/3 of each elytron, 8th interval shorter than the remaining ones.

Ventral surface alutaceous; mesosternum convex, smooth at middle, finely punctate laterally with distinct transverse depression in front of intercoxal carina; space between mesocoxae smaller than width of mesofemur, intercoxal carina narrow, convex; metasternum convex, midline indicated, punctures minute to fine, scattered; lateral metasternal triangle absent; abdominal sternites with large fluting along sutures, in some specimens margins of sternites crenate, surface smooth or minutely punctate; exposed portion of pygidium shiny, minutely punctate.

Legs relatively short; all femora smooth, finely punctate or not punctate; meso- and metatibiae as long as femora; apex of metatibia with small external spine, spurs slender, unequal in length; tarsus shorter than tibia, basal tarsomere shorter than upper tibial spur and shorter than following three tarsomeres combined.

Male. Penultimate abdominal sternite shorter and less arcuate ventrally than in female; genitalia as in Fig. 59.

Female. Elytra usually slightly longer than in male; exposed portion of pygidium shorter than eroded base.

**Type data.** Neotype female, labelled “Neotype *Saprosites sulcatissimus* (Broun 1911) 6/10/58 det. A.M. Richards”, “Pitt Island 16–26.I.44 E.S. Gourlay”, “E.S. Gourlay Acc. 1970 Ent. Div.” (NZAC).

Syntypes (2), same data as neotype (NZAC).

**Material examined.** Type specimens plus 49 non type examples (CMNO, ISEA, LUNZ, NZAC).

– / – / CH.

Collected November to April.

Recorded from nearly all islands of the Chathams.

Found primarily in leaf litter of forest sedges, under fog-grass and in sand. On South East Island the specimens were found in linings of eight nests of *Pachyptila vittata* and *Coenocorypha pucilla*.

**Remarks.** The dark colour, the very deep elytral striae and narrow, subcarinate intervals readily separate *S. sulcatissimus* from the other members of New Zealand *Saprosites*. The species seems to be most closely related to the *S. fortipes-watti* complex. Endemic to the Chatham Islands.

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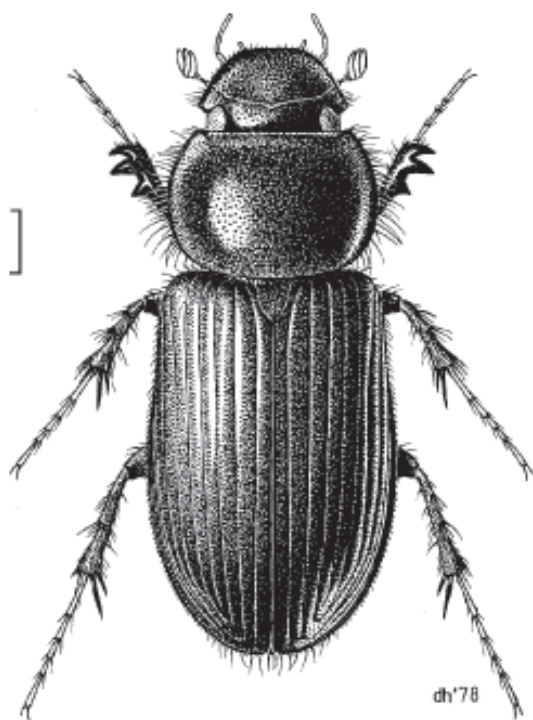
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ILLUSTRATIONS

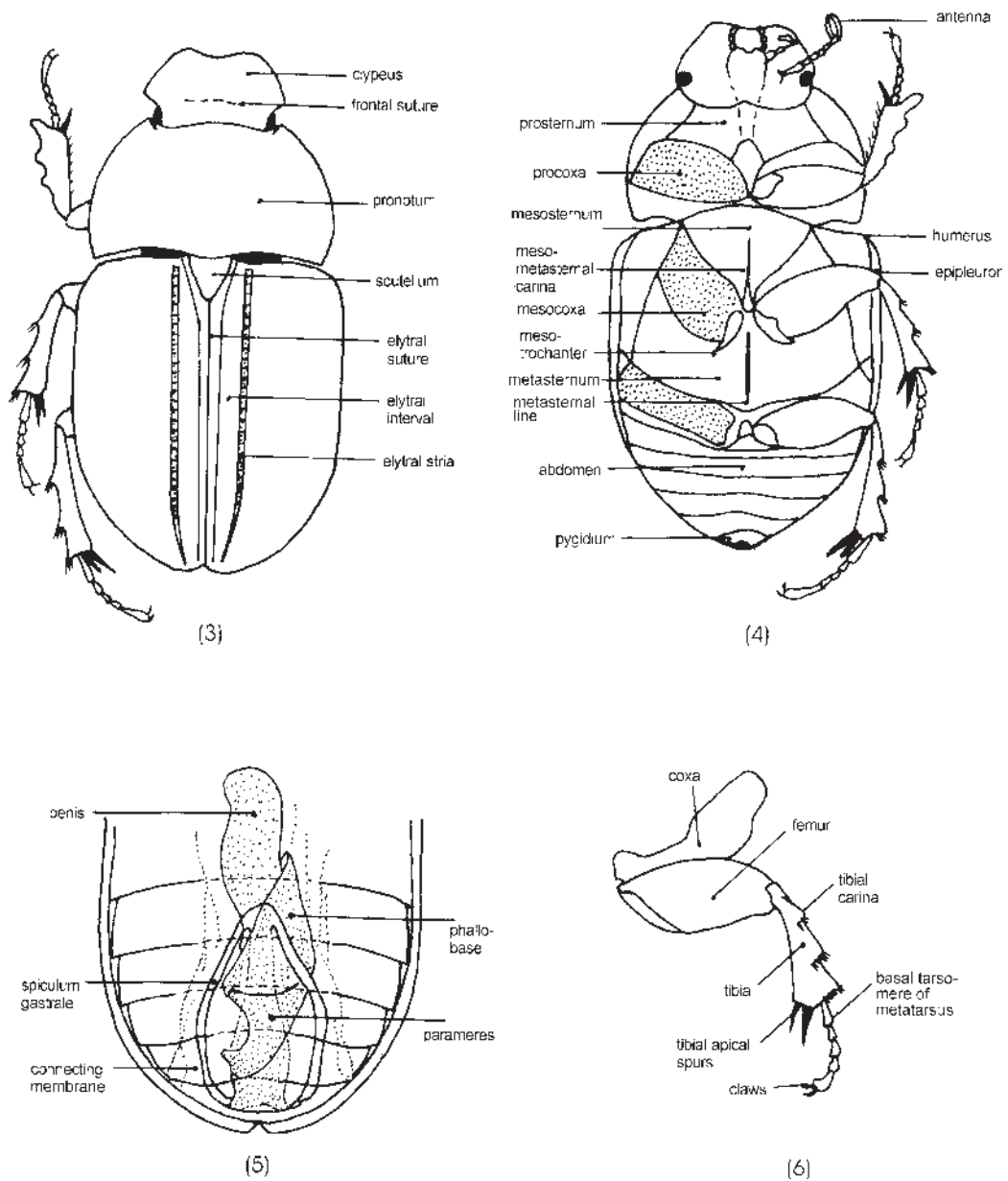


(1) *Acrossidius tasmaniae*

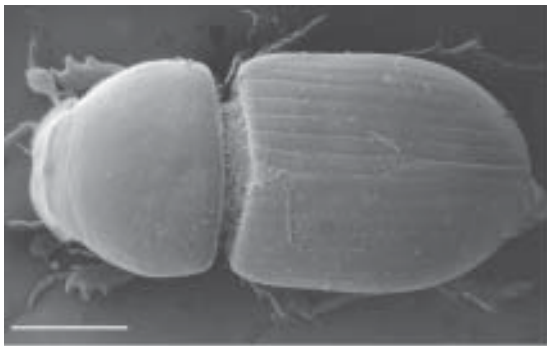


(2) *Phycocus graniceps*

Fig. 1-2 Dorsal habitus: (1) *Acrossidius tasmaniae* (Hope, 1847), illustrator D. W. Helmore; (2) *Phycocus graniceps* Broun, 1886, illustrator A. C. Harris. Scale line = 1 mm.



**Fig. 3–6** *Proctophanes sculptus*, illustrating morphological features of Aphodiinae: (3) Body, dorsal aspect; (4) Body, ventral aspect; (5) Male genitalia, ventral aspect; (6) Hind leg, ventral aspect.



(7) *Aphodius granarius*



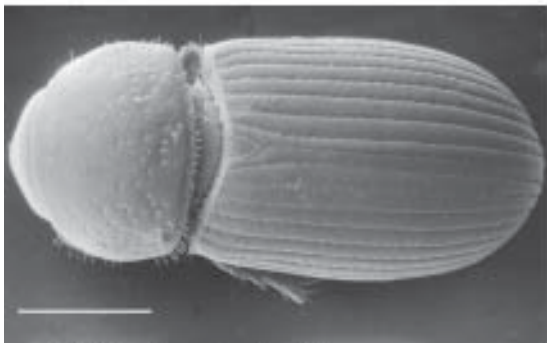
(8) *Tesarius sulcipennis*



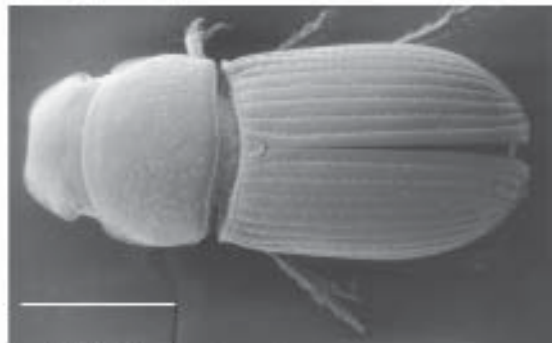
(9) *Proctophanes sculptus*



(10) *Proctophanes minor*

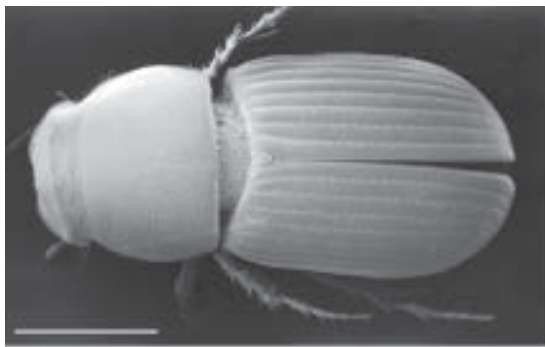


(11) *Parataenius simulator*



(12) *Ataenius brouni*

Fig. 7–12 Body, dorsal habitus. Scale line = 1 mm.



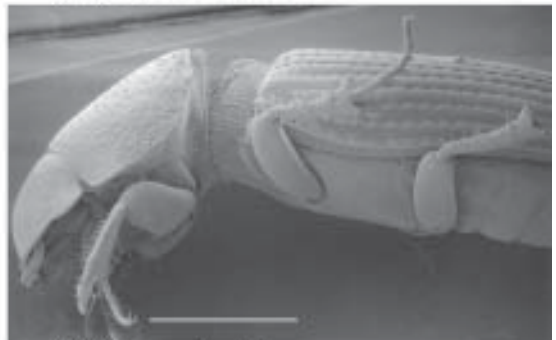
(13) *Australaphodius frenchi*



(14) *Saproscites mendax*



(15) *Saproscites exsculptus*



(16) *Saproscites distans*



(17) *Saproscites raoulensis*



(18) *Saproscites communis*

**Fig. 13–18** (13) Dorsal habitus, *Australaphodius frenchi*; (14–18) Lateral view of head, pronotum, and elytron of *Saproscites* species. Scale line = 1 mm.



(19) *Saproites kingsensis*



(20) *Saproites fortipes*

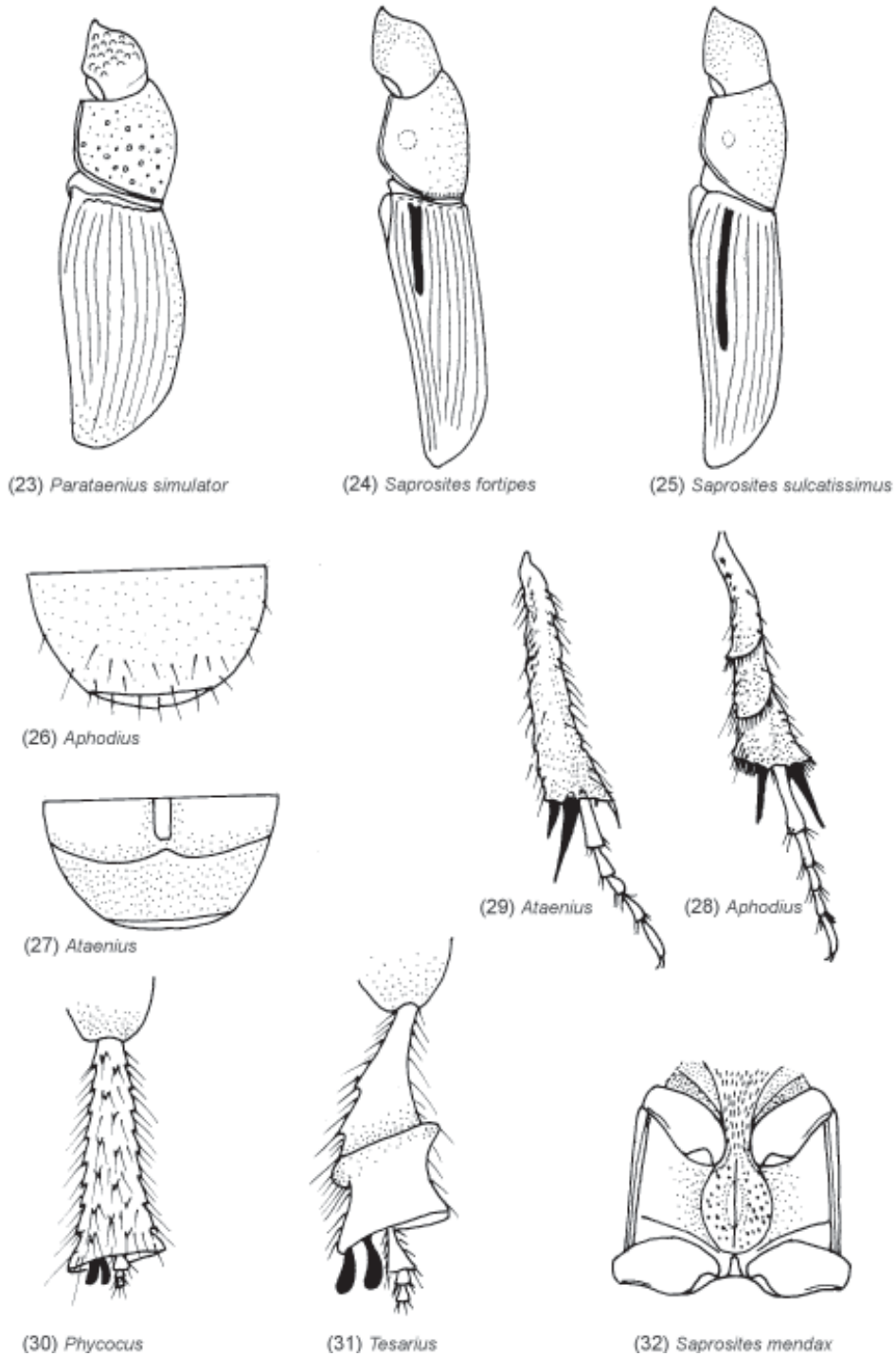


(21) *Saproites watti*



(22) *Saproites sulcatissimus*

Fig. 19–22 Lateral view of head, pronotum, and elytron of *Saproites* species. Scale line = 1 mm.



**Fig. 23–32** (23–25) Head, pronotum, and elytron, lateral view (note elytral intervals); (26–27) Pygidium, dorsal view; (28–31) Metatibia and tarsal segments (note tibial spurs); (32) Mesosternum, *Saproites mendax*.



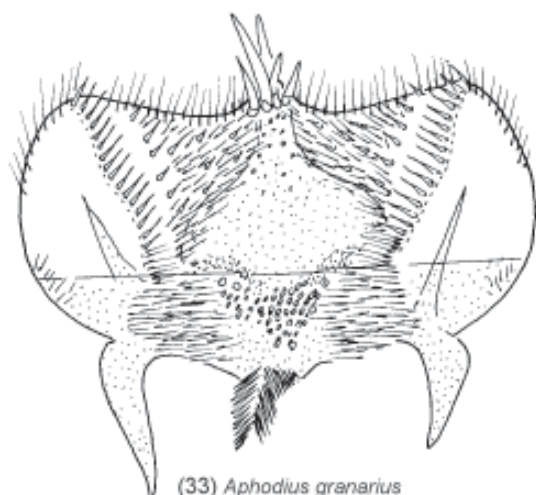
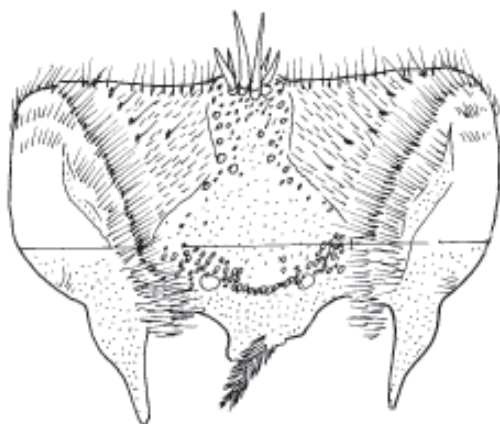
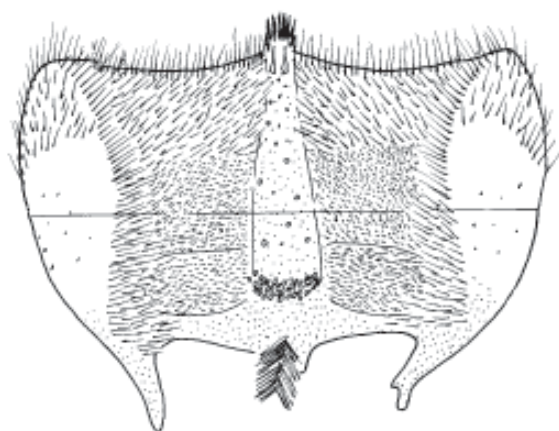
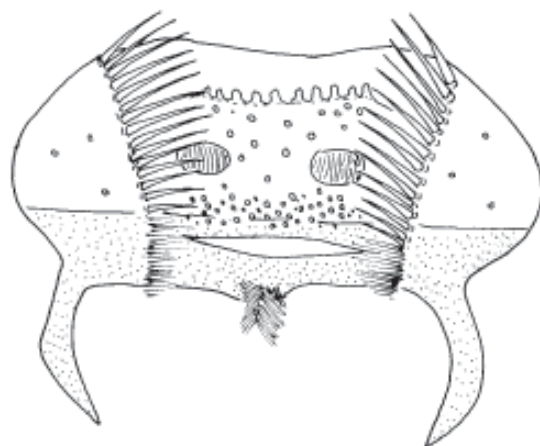
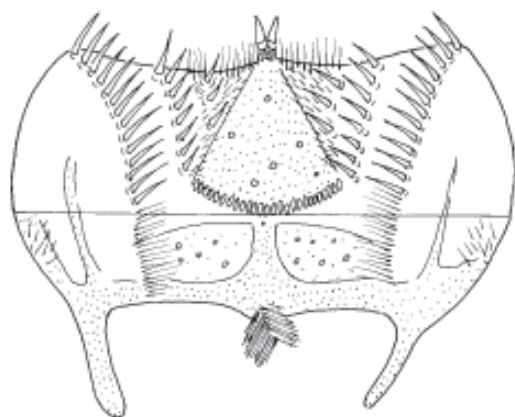
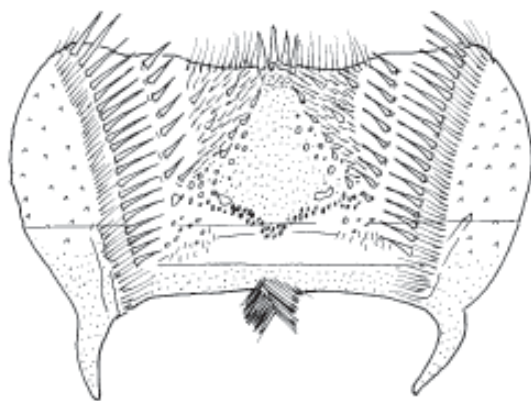
(33) *Aphodius granarius*(34) *Aphodius lividus*(35) *Acrossidius tasmaniae*(36) *Phycocus graniceps*(37) *Proctophanes minor*(38) *Australaphodius frenchi*

Fig. 33–38 Epipharynx.

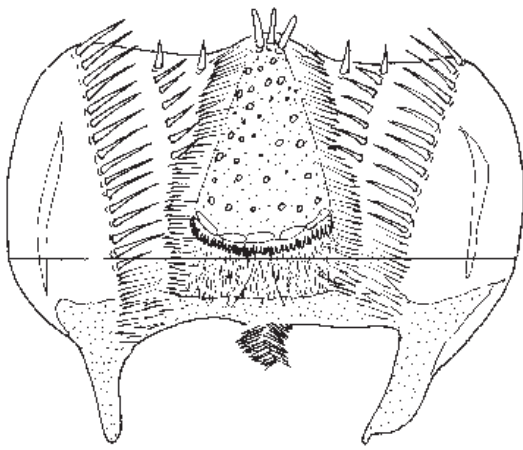
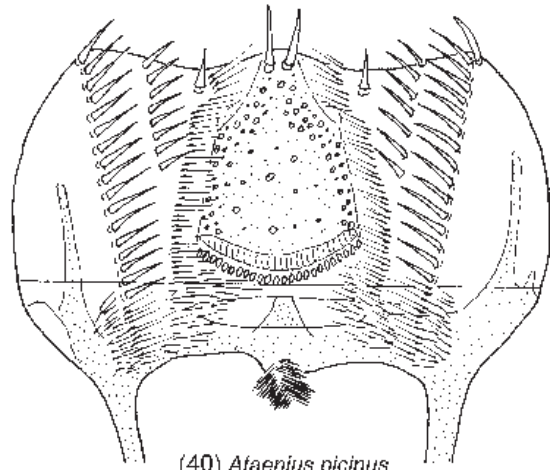
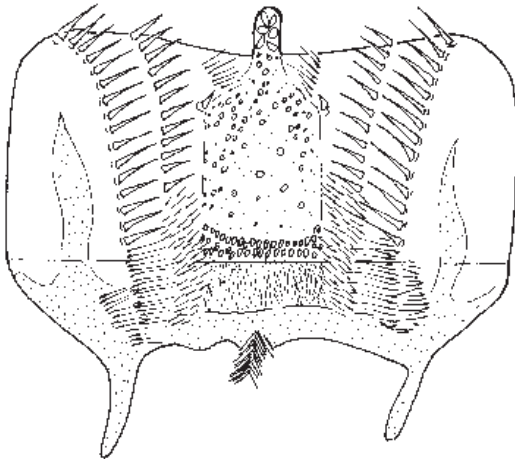
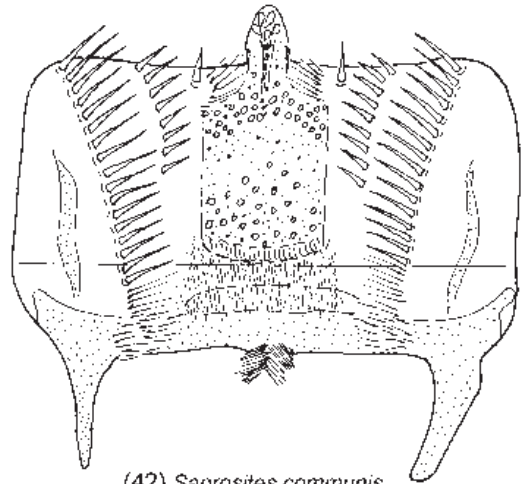
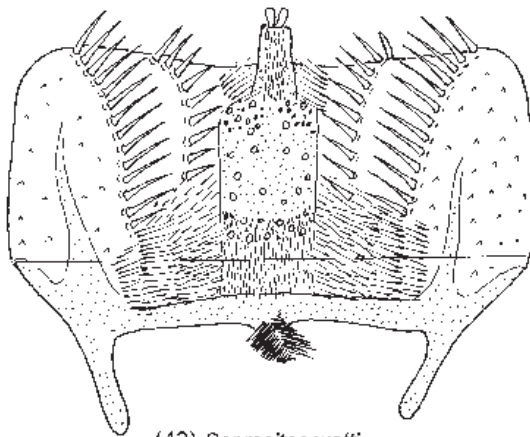
(39) *Ataenius brouni*(40) *Ataenius picinus*(41) *Saproscites distans*(42) *Saproscites communis*(43) *Saproscites waffi*

Fig. 39–43 Epipharynx.

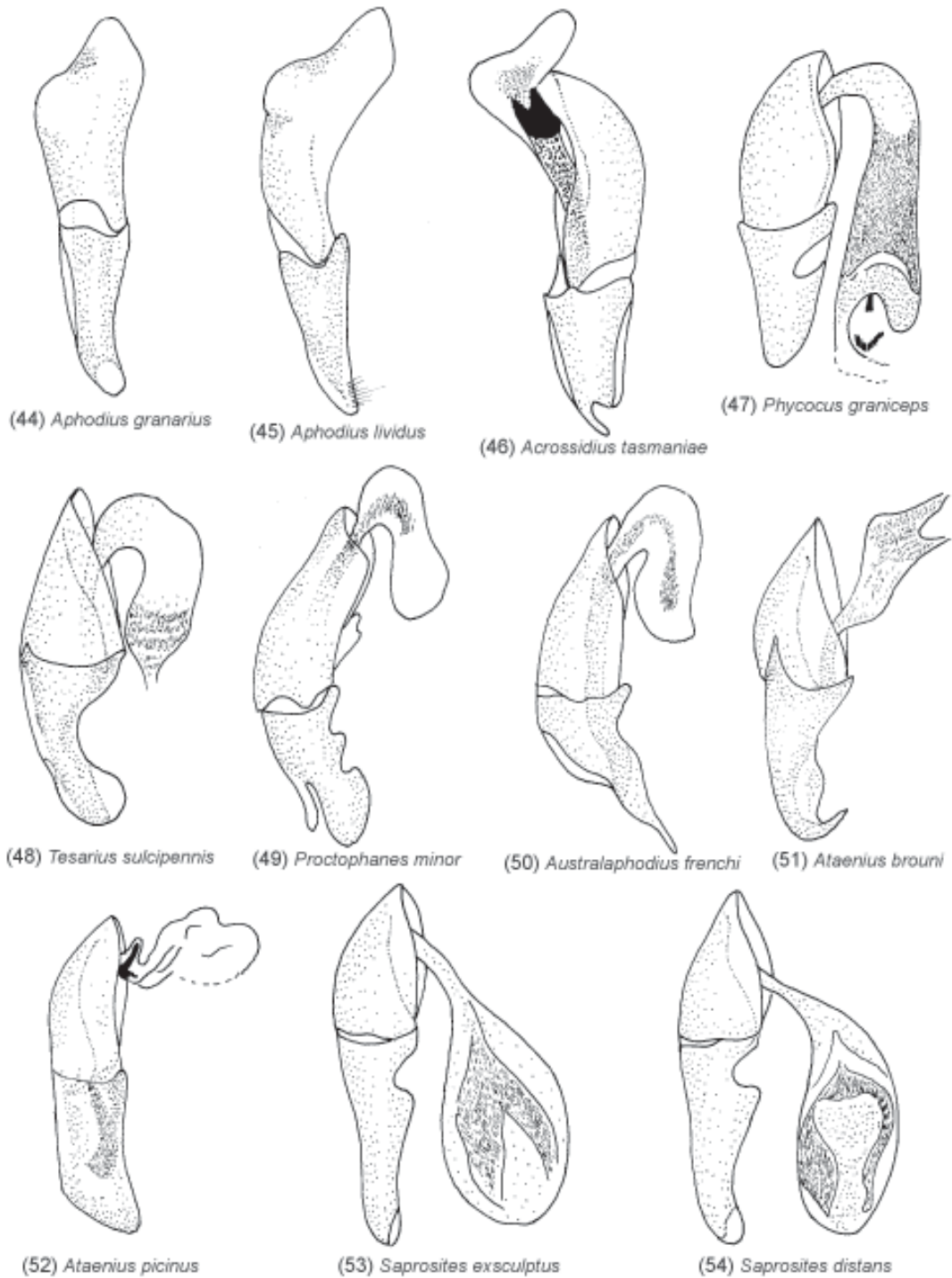
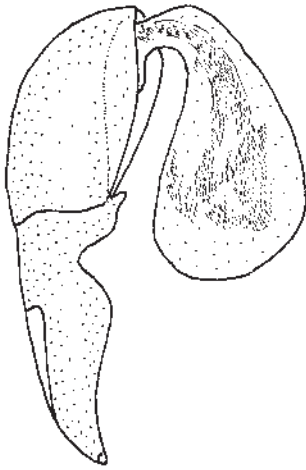
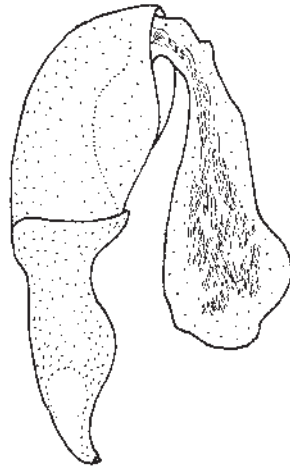
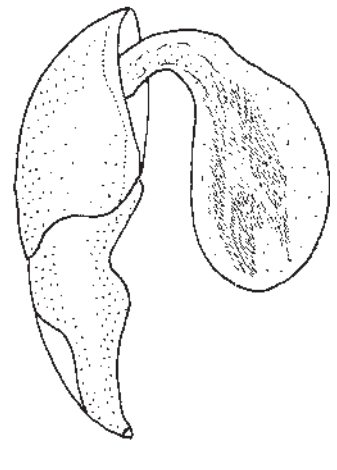
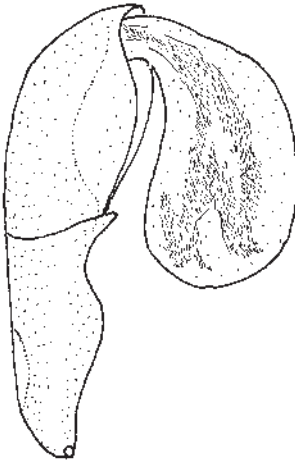
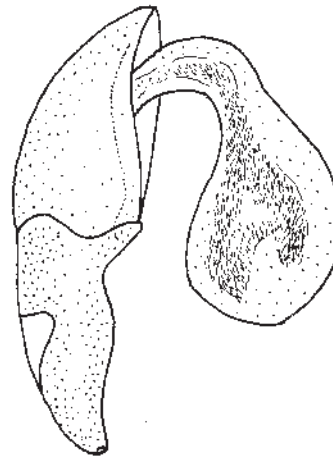
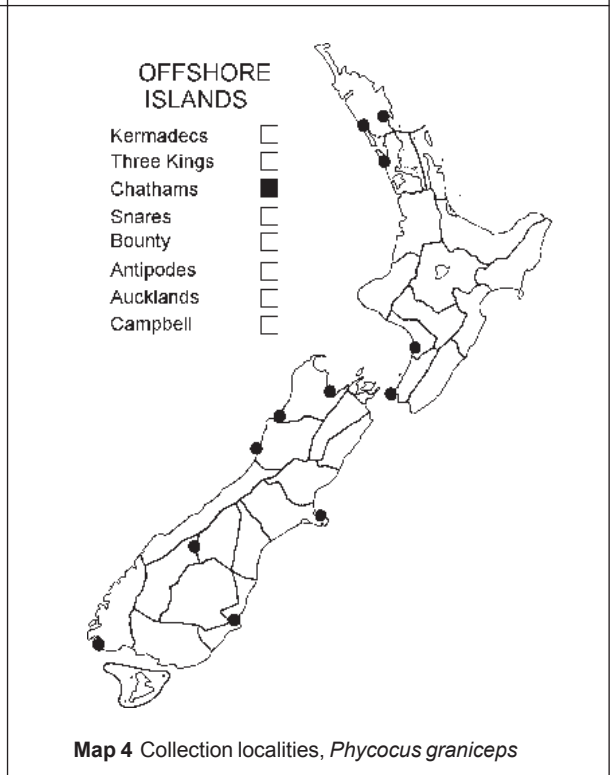
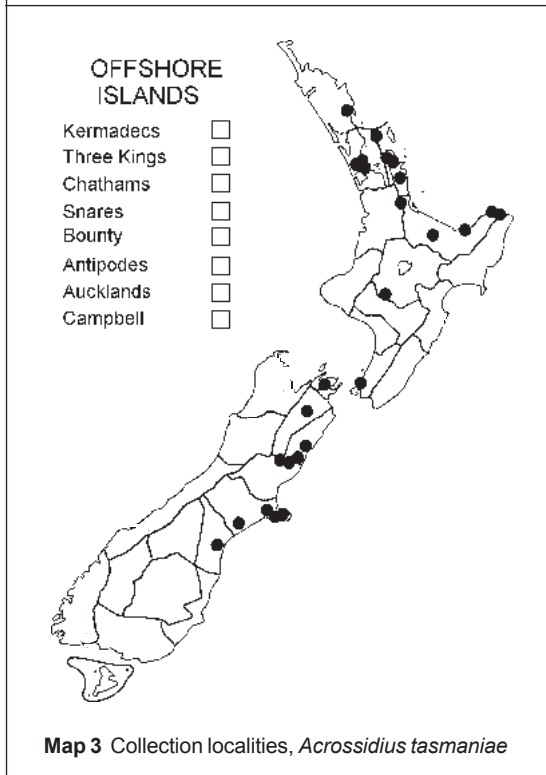
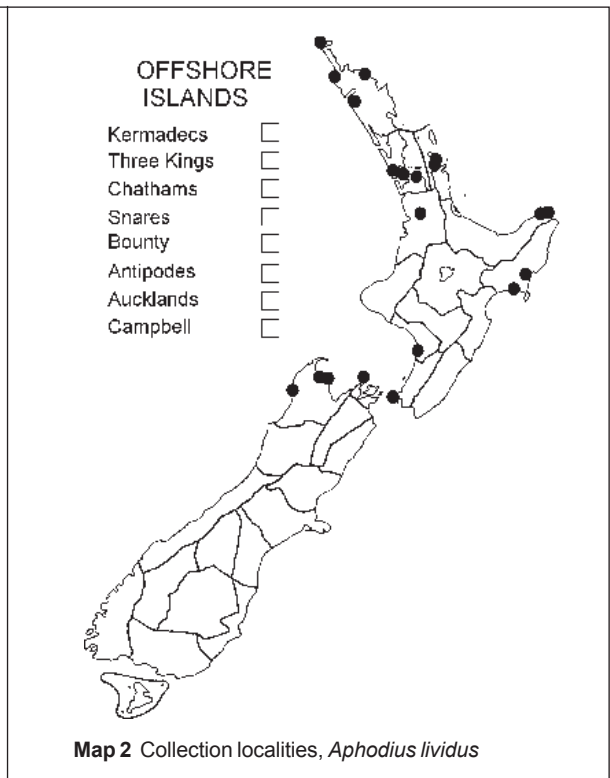
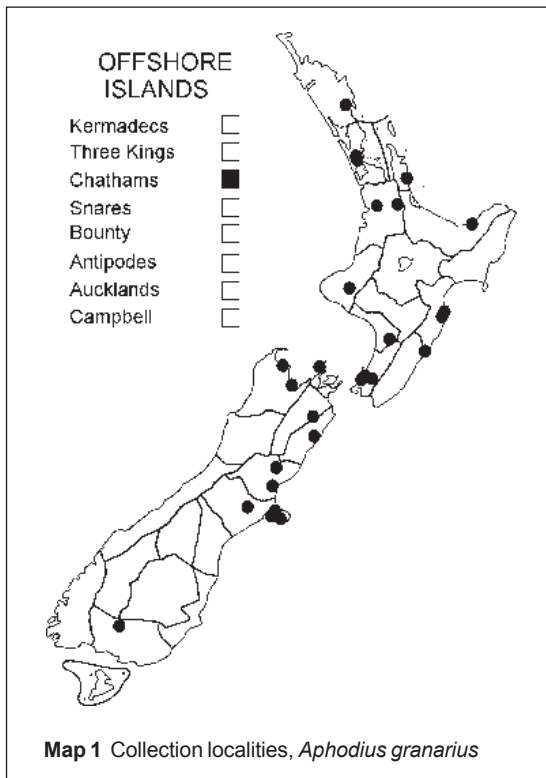
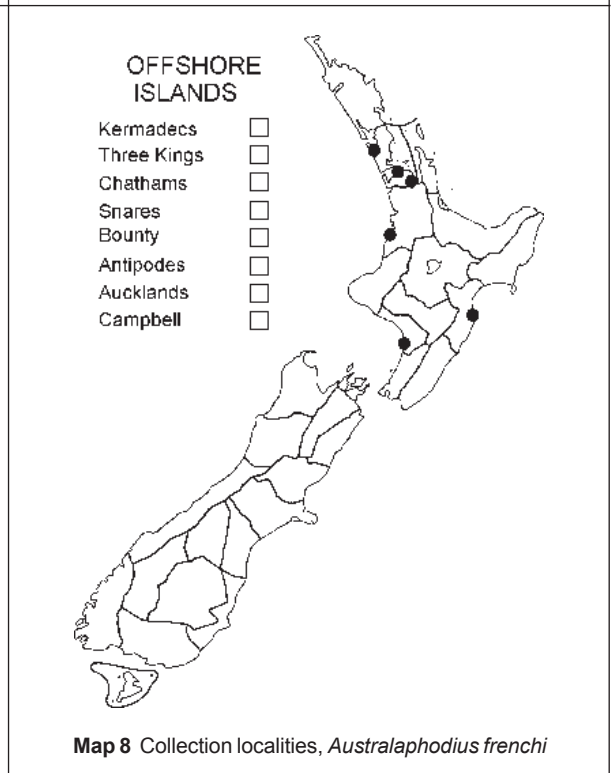
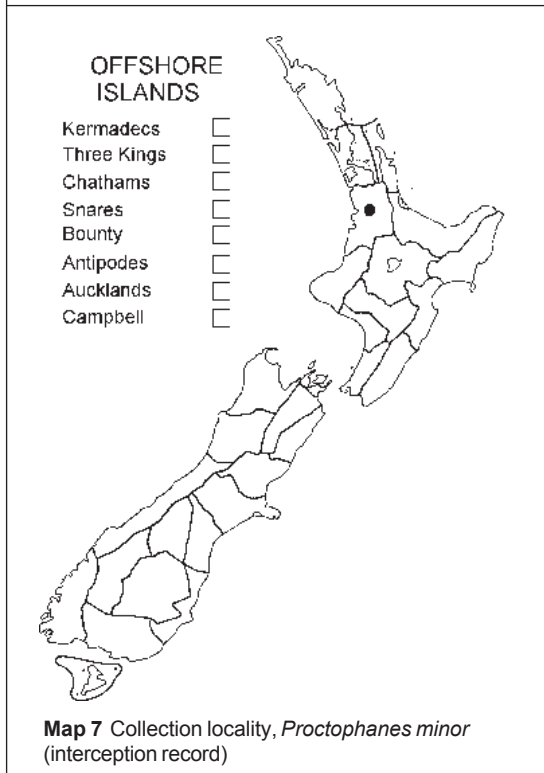
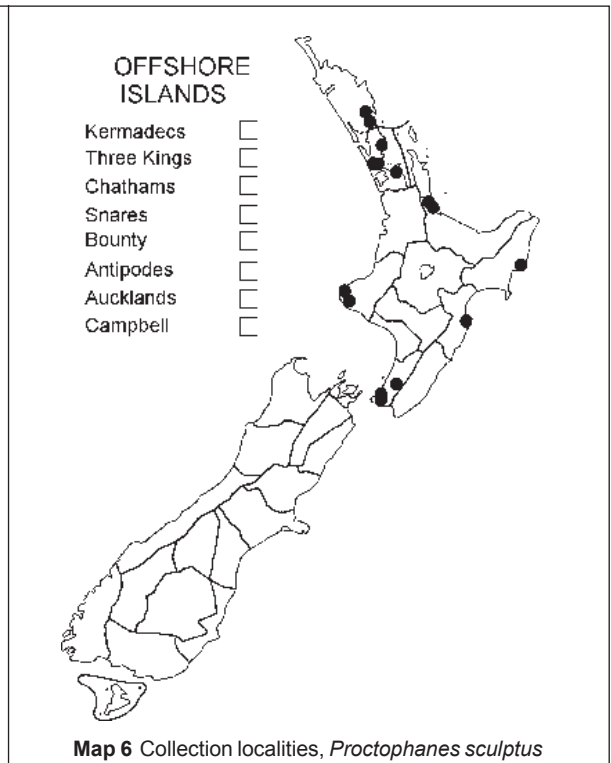
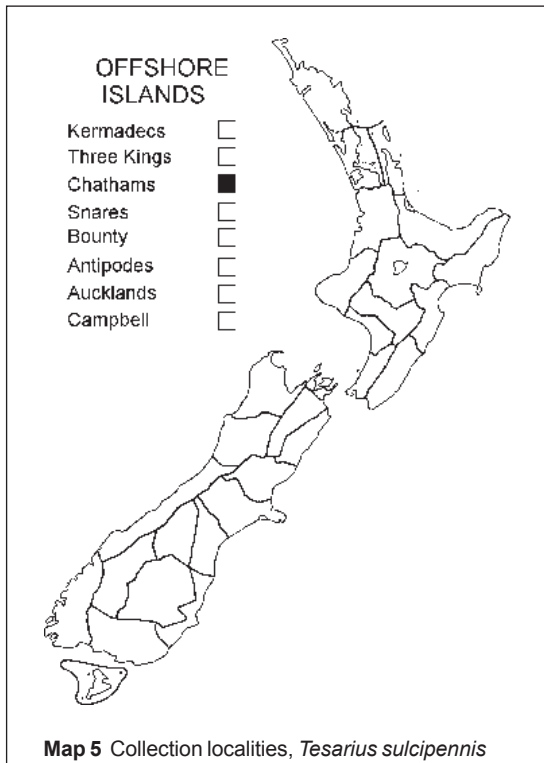
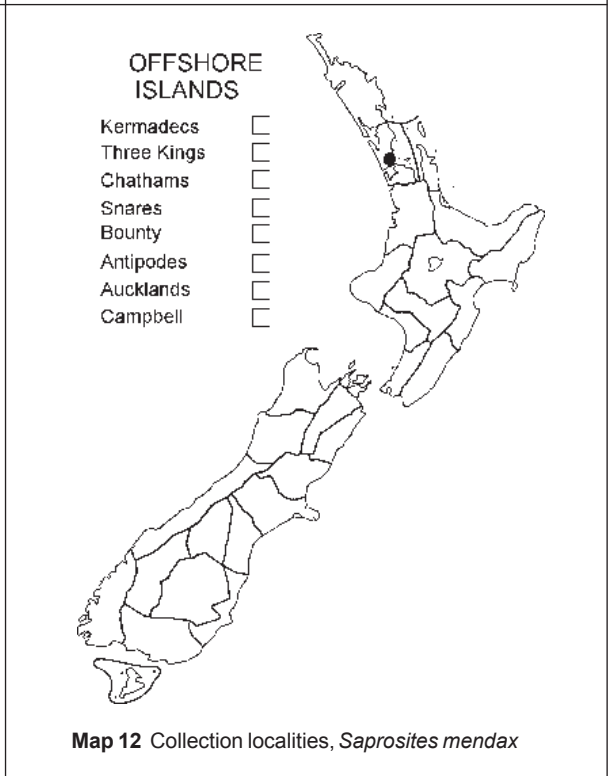
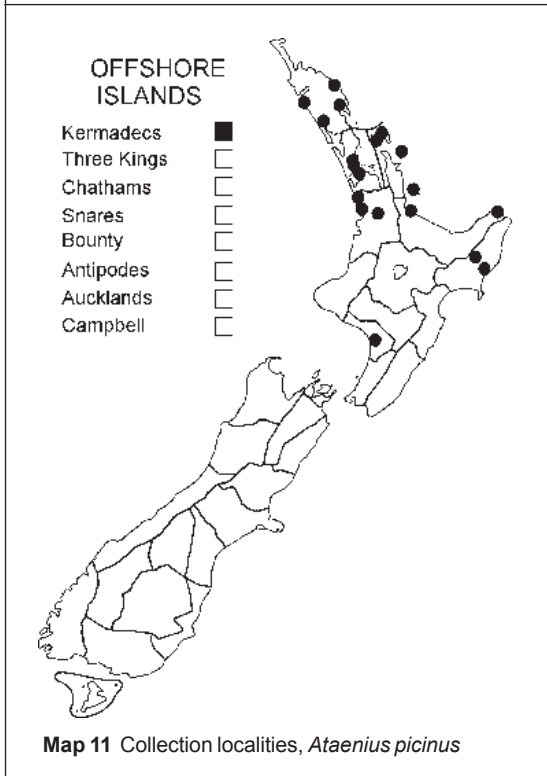
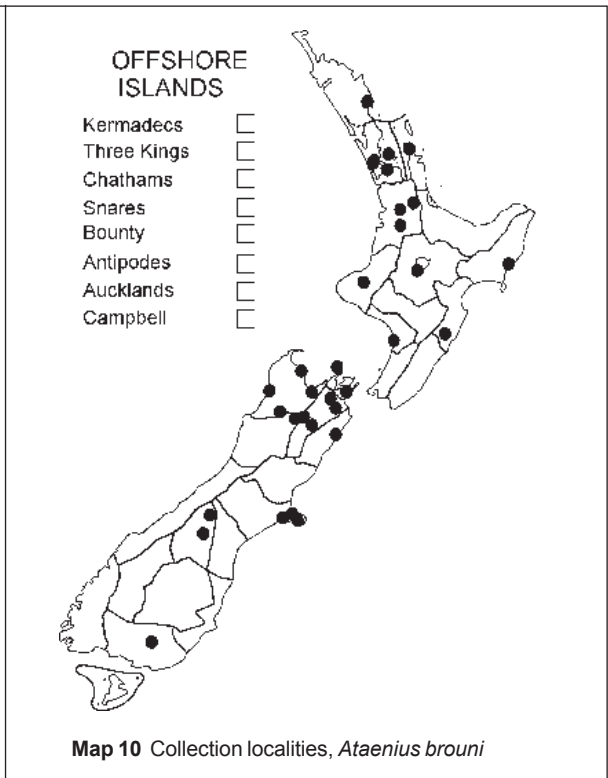
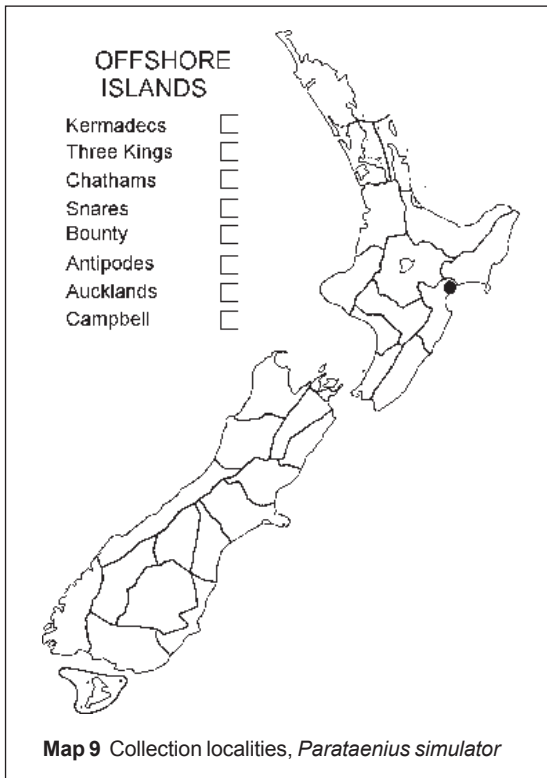


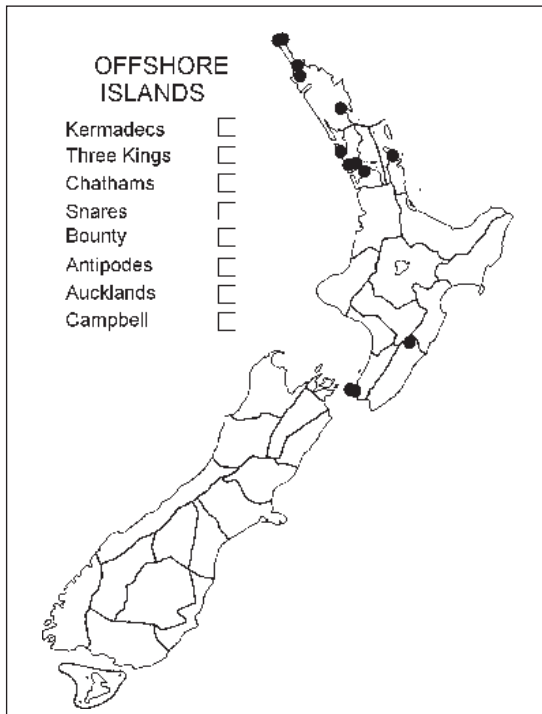
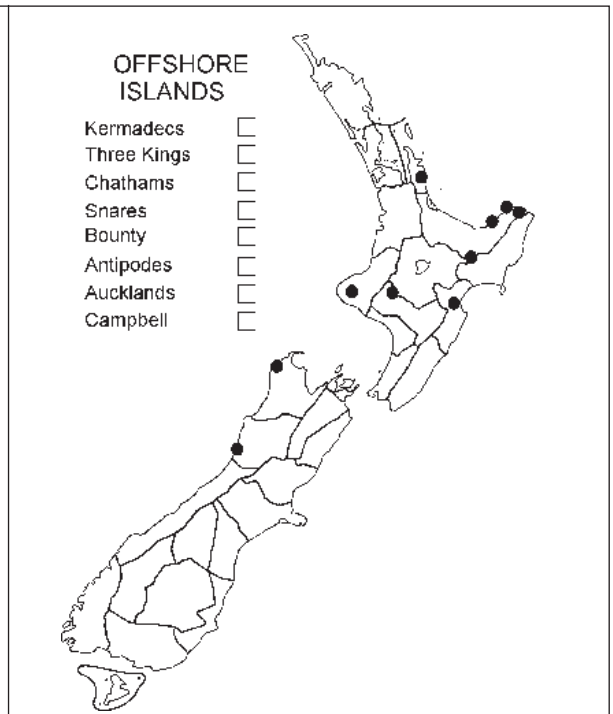
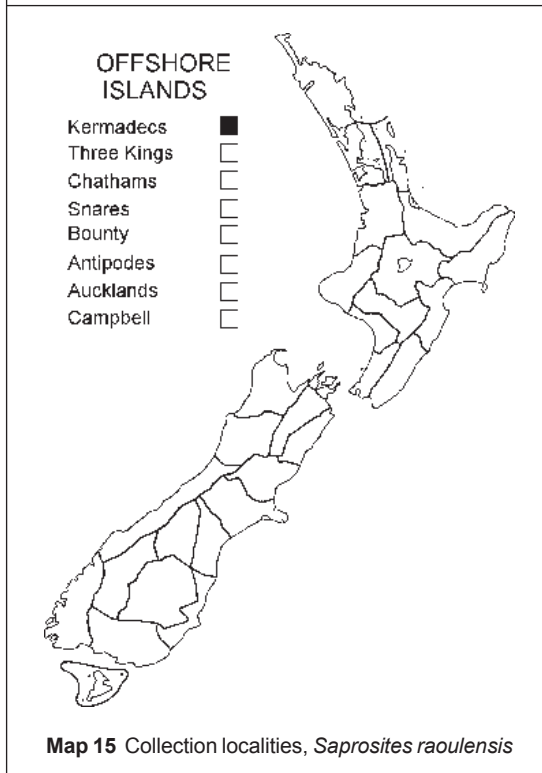
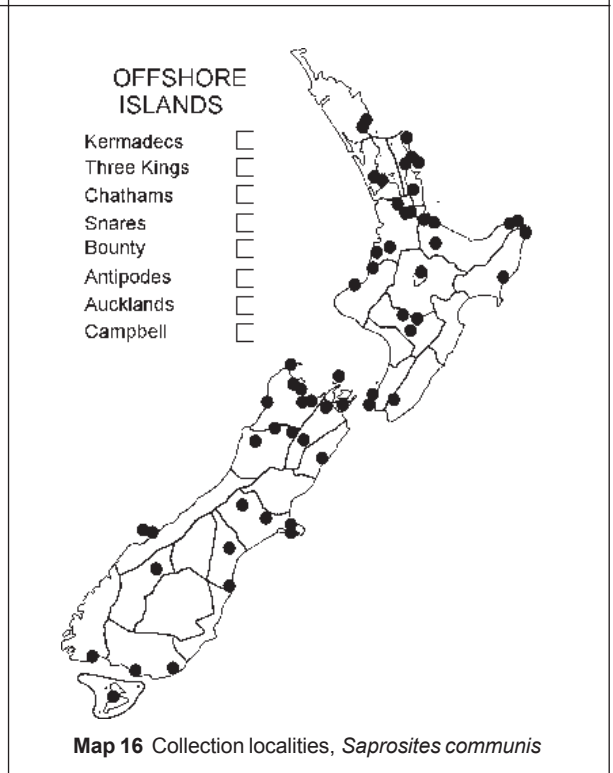
Fig. 44–54 Male genitalia, lateral view.

(55) *Saproites communis*(56) *Saproites kingsensis*(57) *Saproites fortipes*(58) *Saproites watti*(59) *Saproites sulcatissimus***Fig. 55–59** Male genitalia, lateral view.

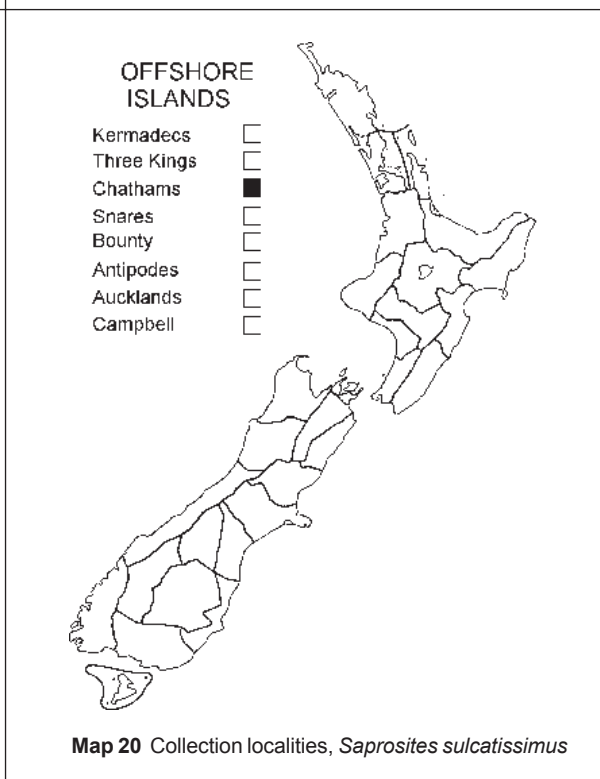
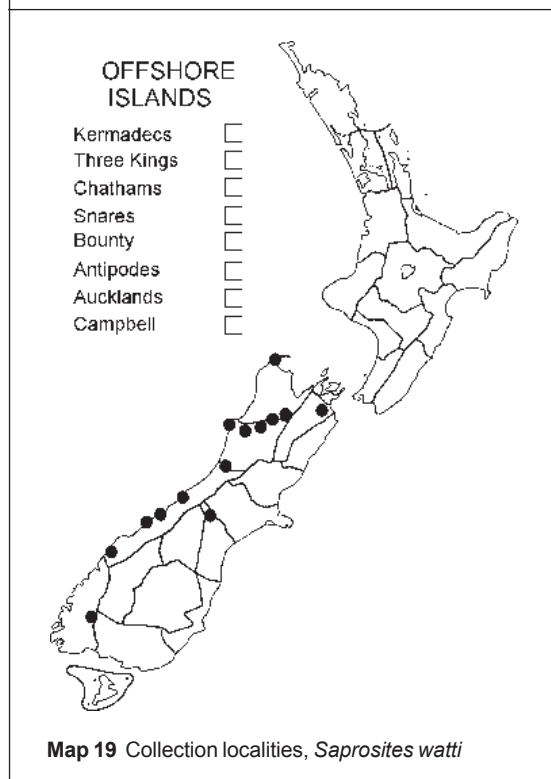
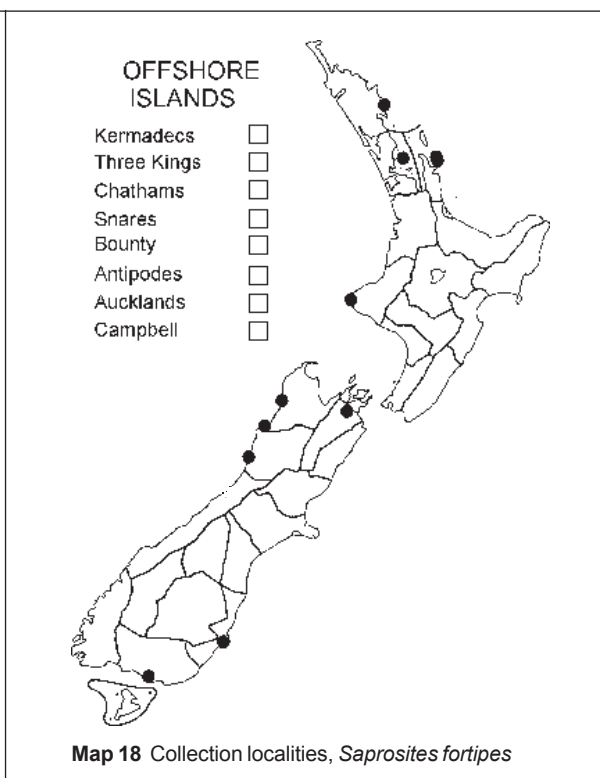
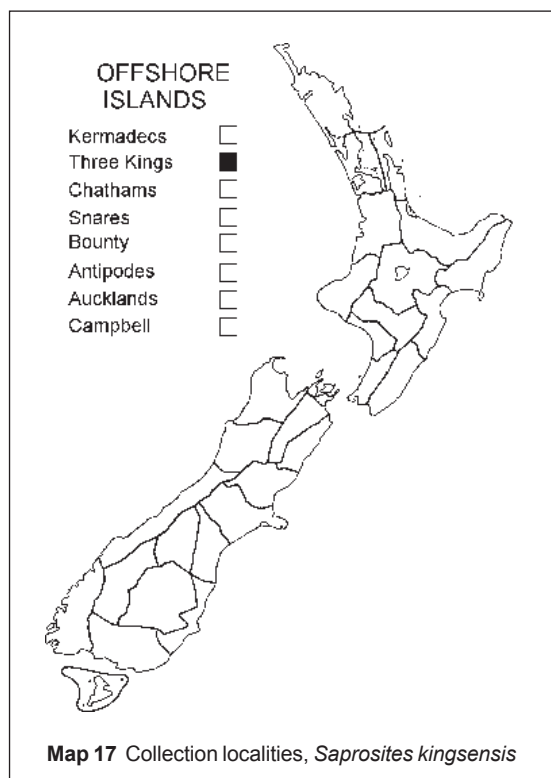






Map 13 Collection localities, *Saprosites exsculptus*Map 14 Collection localities, *Saprosites distans*Map 15 Collection localities, *Saprosites raulensis*Map 16 Collection localities, *Saprosites communis*



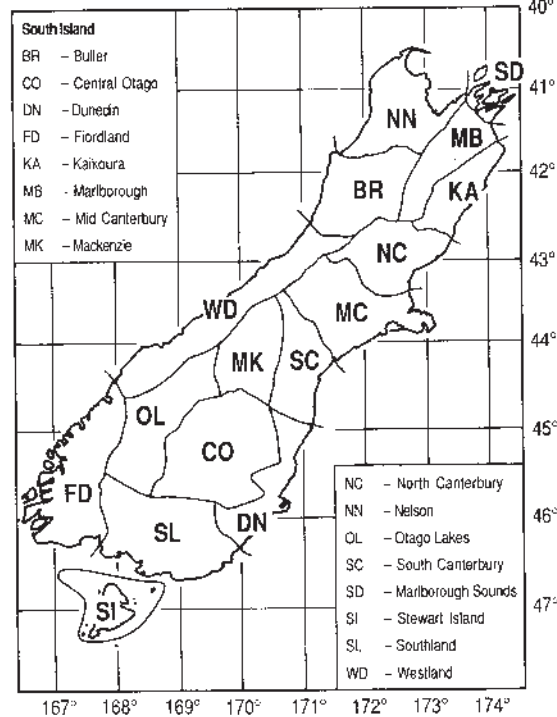
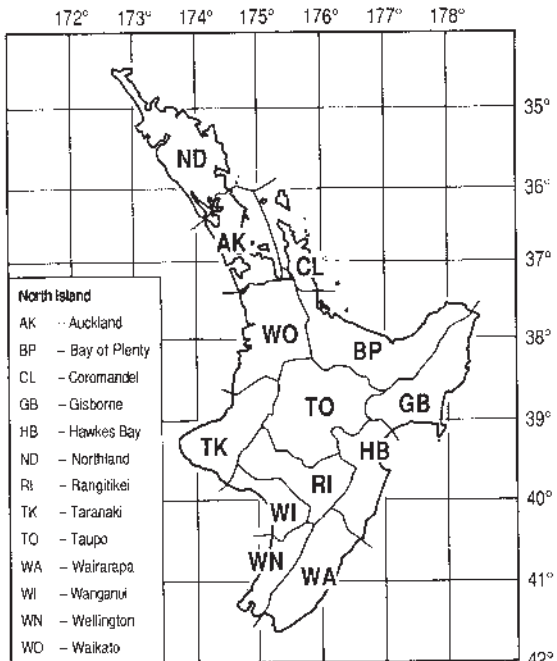


## TAXONOMIC INDEX

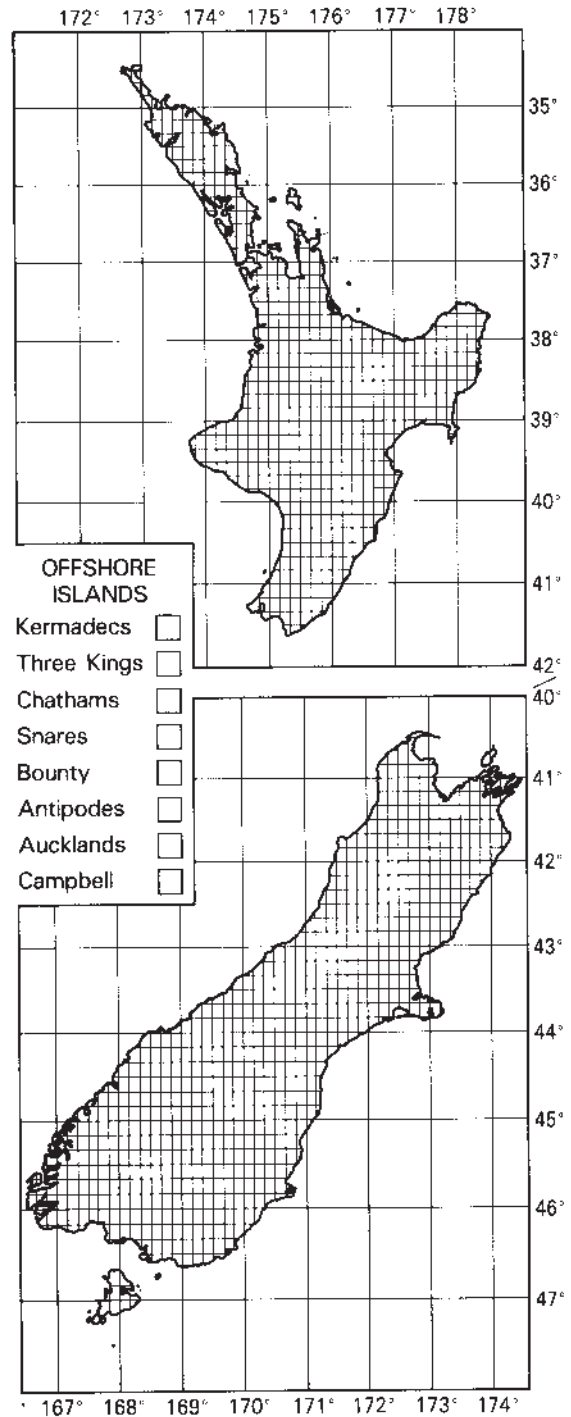
Page numbers in **bold** type denote a description, and in *italic* type illustrations. A suffixed letter 'k' indicates a key, and 'm' a map.

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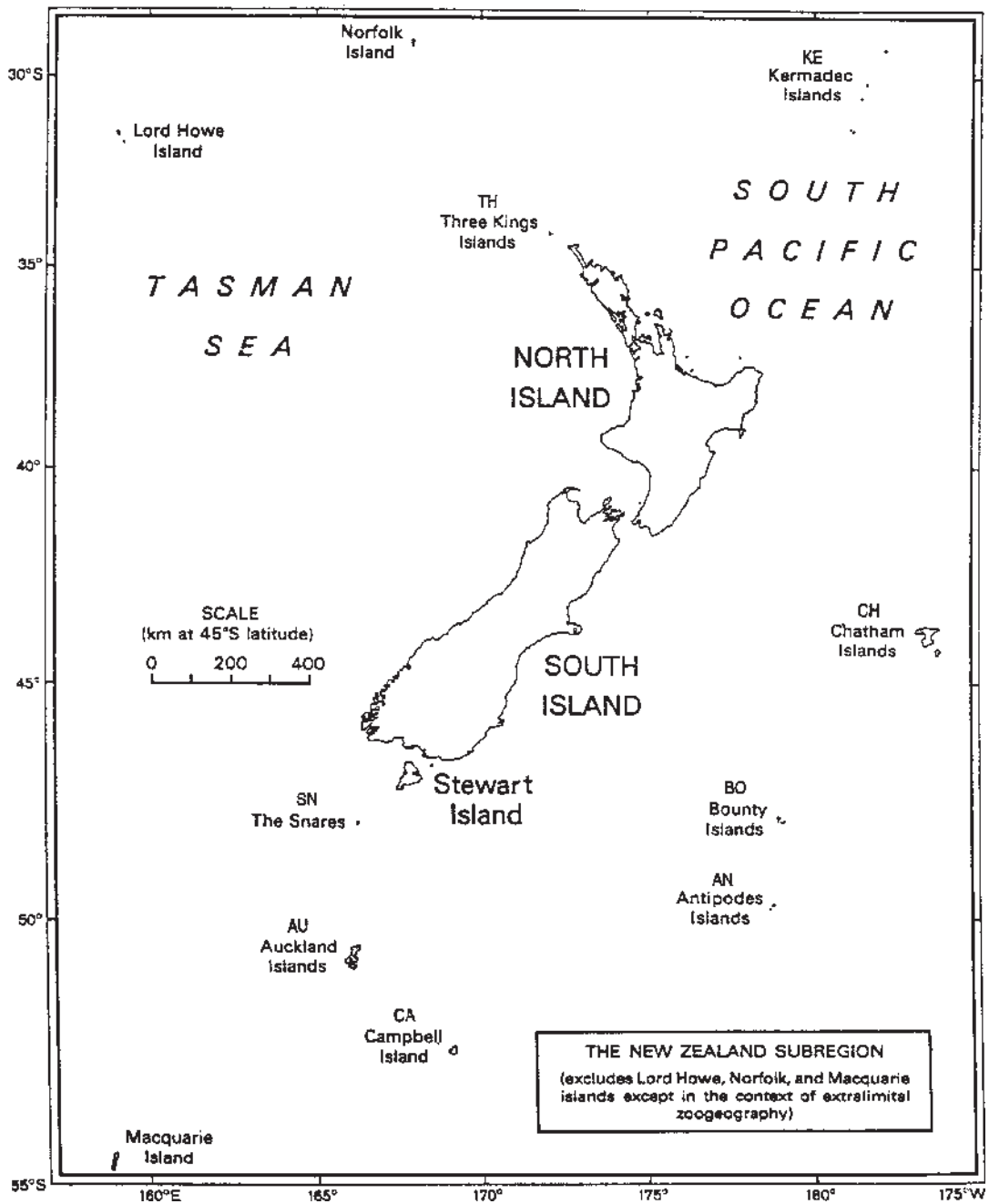
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Area codes and boundaries used to categorise specimen locality data (after Crosby *et al.* 1998)



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He titiro wh~iti t~ t'nei pukapuka ki ng~ mea noho whenua, kōre he tuar~; i p'nei ai i te mea kei te mōio wh~nuitia ng~mea whai tuar~; ko ng~mea noho moana, koir~te tino kaupapa o te huinga pukapuka *Marine Fauna of N.Z.*

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Me wh~ki te kaituhi i tōa whakaaro ki t' tahi o te K~hui } rahi Whakarōāanga Tuar~Kore, ki te •tita r~nei i mua i te tōnatanga, ~, m~r~tou a ia e ~rahi mōte w~hi ki tana tuhinga.

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Te utu (tirohia "Titles in print", wh~rangi 62). Ko te kōpaki me te pane kuini kei roto i te utu. Me utu te hunga e noho ana i Aotearoa me Ahitereiria ki ng~t~ra o Aotearoa. Ko t' tahi atu me utu te moni kua tohua, ki ng~t~ra Merikana, ki te nui o te moni r~nei e rite ana.

E toe ana he pukapuka o ng~putanga katoa o mua. Mehemea e hiahia ana koe ki te katoa o ng~pukapuka, ki t' tahi r~nei, tonoa mai kia whakaheke te utu. Tekau tōa te heke iho o te utu ki ng~toa hoko pukapuka.