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Wing Development and Evolution of New Zealand Lucanidae (Insecta: Coleoptera)

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Abstract

THIRTEEN flightless and 13 fully winged species of Lucanidae occur in the New Zealand area. The vestigial hindwings of the six New Zealand species referred to *Dorcus* Macleay are illustrated and compared with those of the fully winged *D. parallelipipedus* (Linn.) from Europe, and those of the seven New Zealand species placed in *Lissotes* Westwood also are illustrated and discussed. Illustrations of the fully developed wings of *Dendroblax* White (monotypic) and of two of the 12 New Zealand species of *Ceratognathus* Westwood are given. Generic differences are apparent in the proportions of the hindwings of fully winged lucanids. In vestigial wings the apex moves towards the base of the costa, the posterior margin moves towards the costal margin, there is a general overall decrease in the size of the wing, the veins become weak, and long setae may become numerous on parts of the wing. Within a group of related species the wings atrophy at different rates and to different extents. The flight wings of one species of *Ceratognathus* are beginning to atrophy. Ancestors of all the existing New Zealand lucanid groups probably arrived in the area as fully winged species. Distribution maps show that flightless genera tend to have localized allopatric species which characteristically occur in lowland areas, whereas fully winged genera have widespread sympatric species, some of which are confined to montane regions. Speciation in the flightless genera seems to have resulted mainly from isolation on islands and in ice-free refuges of populations of widespread, flightless species. The New Zealand species of *Ceratognathus* probably have evolved from at least three colonizing Australian species, and the group is divided into montane and lowland species, as well as into large- and small-sized species which are closely related. Some of the New Zealand species of *Lissotes* appear to have been evolving since at least the last Interglacial (about 70,000 to 150,000 years ago) and perhaps since or during the Pliocene. *Dorcus* has the appearance of being an older group than *Lissotes* in New Zealand. *Dendroblax earlii* White is related to lucanids in Australia, New Guinea, Lord Howe Island and Chile, and is probably an old, plastic species in New Zealand.

INTRODUCTION

SINCE Wollaston (1854) reported his discovery that the hindwings are atrophied in one-third of the native species of beetles on Madeira it has generally been assumed that secondarily flightless insects are more numerous on islands than elsewhere. Published statistics to show that this assumption is correct are not

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readily available. Darlington (1936) has discussed some aspects of wing atrophy in carabid beetles of Eastern North America, and in a later paper (Darlington, 1943) has shown that flightless Carabidae are more abundant on mountains and on high islands in cool regions than they are on lowlands of continents and on low tropical islands. For most other families of insects precise information on the morphology of atrophied wings and on the numbers of flightless and fully winged species that occur on islands and continents has not been published.

In the New Zealand area many families of insects contain secondarily flightless species; in Coleoptera, for instance, species with atrophied wings occur in Anthribidae, Carabidae, Cerambycidae, Colydiidae, Curculionidae, Elateridae, Lucanidae, Scarabaeidae and Tenebrionidae. Also, some New Zealand species of Hemiptera, especially those living in leaf litter and moss on the forest floor, have vestigial wings, and most of the endemic New Zealand species of Orthoptera are flightless. To date, however, the extent to which flightlessness occurs in New Zealand insects is very incompletely recorded.

The present paper deals with the New Zealand species of one family of beetles, the Lucanidae. As a whole, the family is a small one, having throughout the world only about 1,000 species at the present time, and in terms of numbers of species it is very insignificant in the New Zealand area. However, the New Zealand lucanids constitute a particularly interesting group in that they include flightless as well as fully winged species. The 26 endemic species belong to four genera; two of these are flightless and contain 13 species; the other two are made up of 13 species, all of which are fully winged. The following topics are discussed in this paper:

(1) Morphology of the hindwings of fully winged and vestigial winged species.

(2) Distribution of the species and genera.

(3) Probable history of the species and genera.

METHODS AND TERMINOLOGY

The left hindwing together with a small part of the metatergum was removed from each specimen examined, and was stored in glycerine in a genitalia vial accompanying the specimen. For most specimens the wings were examined, measured, and drawn in a small dish of alcohol under a stereoscopic microscope, but some temporary slide mounts in glycerine were also prepared. Illustrations of the wings were made with the aid of either a camera lucida or a squared optical disc.

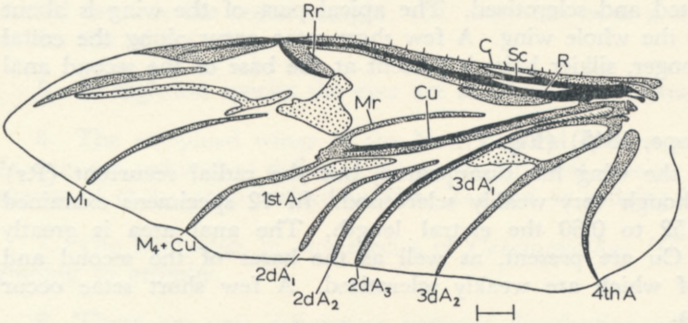
Wing length is measured from the base of the costa to the apex of the wing. The terminology used in naming the veins is that of Forbes (1922). The "apical part" of the wing means that part distal to the radial recurrent vein.

MORPHOLOGY OF THE HINDWINGS

The venation of the hindwings of fully winged species dealt with in this paper is similar to that described by Forbes (1922) for *Lucanus dama* Fab., 1775 (= *L. capreolus* Linn., 1763, according to Benesh, 1960). Characteristically for the family the hindwing has few cross-veins or cells, and the radical recurrent and medial recurrent are conspicuous veins. In the flightless species the hindwings are extremely small and have only a few veins.

Genus DORCUS Macleay, 1819

The six endemic New Zealand species referred to this genus (Holloway, 1961) have atrophied wings. *D. parallelipipedus* (Linn.), the type species, is fully



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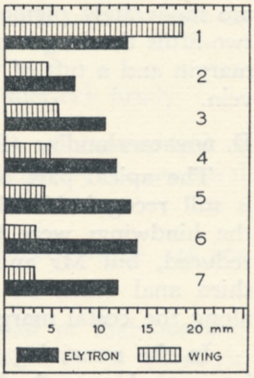

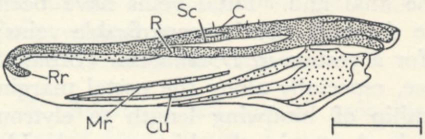

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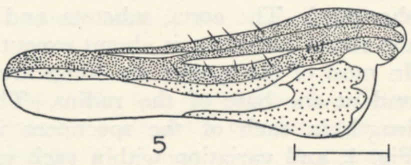

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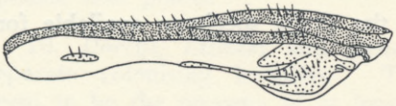

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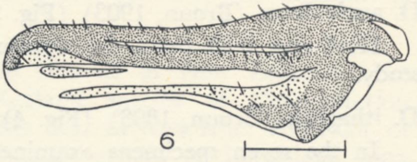

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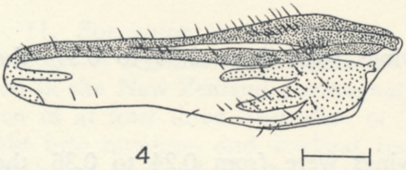

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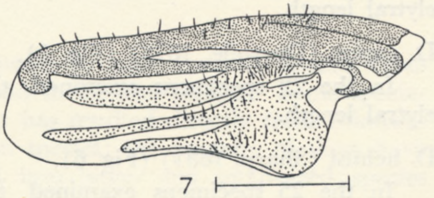

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FIG. 1.—Flying wing of *Dorcus parallelipipedus* ♂ (Italy).

FIGS. 2–7.—Vestigial hindwings of New Zealand species of *Dorcus*. (2) *D. novaezealandiae* ♂ (Wellington); (3) *D. auriculatus* ♀ (Waikato); (4) *D. ithaginis* ♂ (Mokohinau Is.); (5) *D. capito* ♂ (Chatham Is.); (6) *D. helmsi* ♂ (Owen I., Stewart I.); (7) *D. philpotti* ♂ (Hump Ridge).

Histogram shows relationship of hindwing length to elytron length in each of the specimens illustrated (Figs. 1–8). (Scales beside figures equal 1.0mm.) Abbreviations: 1stA, 4thA, first and fourth anal veins; 2dA$_1$, 2dA$_2$, 2dA$_3$, branches of second anal vein; 3dA$_1$ 3dA$_2$, branches of third anal vein; C, costa; Cu, cubitus; M$_1$, M$_4$, branches of media; Mr, medial recurrent; R, radius; Rr, radial recurrent. Axillary sclerites not shown. In Figs. 2–7 the basal edge of the anal area is folded under. Black indicates deep pigmentation; close stipple indicates moderate pigmentation; sparse stipple indicates weak pigmentation; clear areas indicate wing membrane.

winged and does not occur outside Europe and North Africa, but it has been included in the present study for comparative purposes.

D. parallelipipedus (Linnaeus, 1758) (Fig. 1).

The flight wings are strongly developed and about 1.4 times longer than the elytra (see histogram beside Fig. 1). The base of the wing is broad, and the posterior margin is more or less parallel with the costal margin so that the entire wing shape is somewhat rectangular. Venation is complete and most of the veins are moderately pigmented and sclerotized. The apical part of the wing is about two-fifths the length of the whole wing. A few short setae occur along the costal margin and a tuft of longer, silkier hairs is present at the base of the second anal vein.

D. novaezealandiae (Hope, 1845) (Fig. 2).

The apical part of the wing has disappeared, but the radial recurrent (Rr) is still recognizable although very weakly sclerotized. In 12 specimens examined the hindwings were 0.52 to 0.60 the elytral length. The anal area is greatly reduced, but Mr and Cu are present, as well as the bases of the second and third anal veins, all of which are weakly sclerotized. A few short setae occur along the costal margin.

In the remaining five New Zealand species the posterior margin of the wing has moved towards the costal margin and the anal and cubital veins have been shortened. The costa, subcosta and radius are the only clearly recognizable veins; the radial recurrent is absent except perhaps for a vestige in *D. ithaginis* (Broun). In most of the species the wings are very setose, especially along the costal margin and at the base of the radius. The relationship of hindwing length to elytron length in each of the specimens illustrated is shown in the histogram beside Fig. 1, and variation within each species is given below.

D. auriculatus (Broun, 1903) (Fig. 3).

Hindwing 0.53 times the elytron length in the single specimen available for study.

D. ithaginis (Broun, 1893) (Fig. 4).

In the seven specimens examined the hindwings were from 0.41 to 0.56 the elytral length.

D. capito (Deyrolle, 1873) (Fig. 5).

In the 22 specimens examined the hindwings were from 0.30 to 0.37 the elytral length.

D. helmsi (Sharp, 1881) (Fig. 6).

In the 25 specimens examined the hindwings were from 0.24 to 0.36 the elytral length.

D. philpotti (Broun, 1914) (Fig. 7).

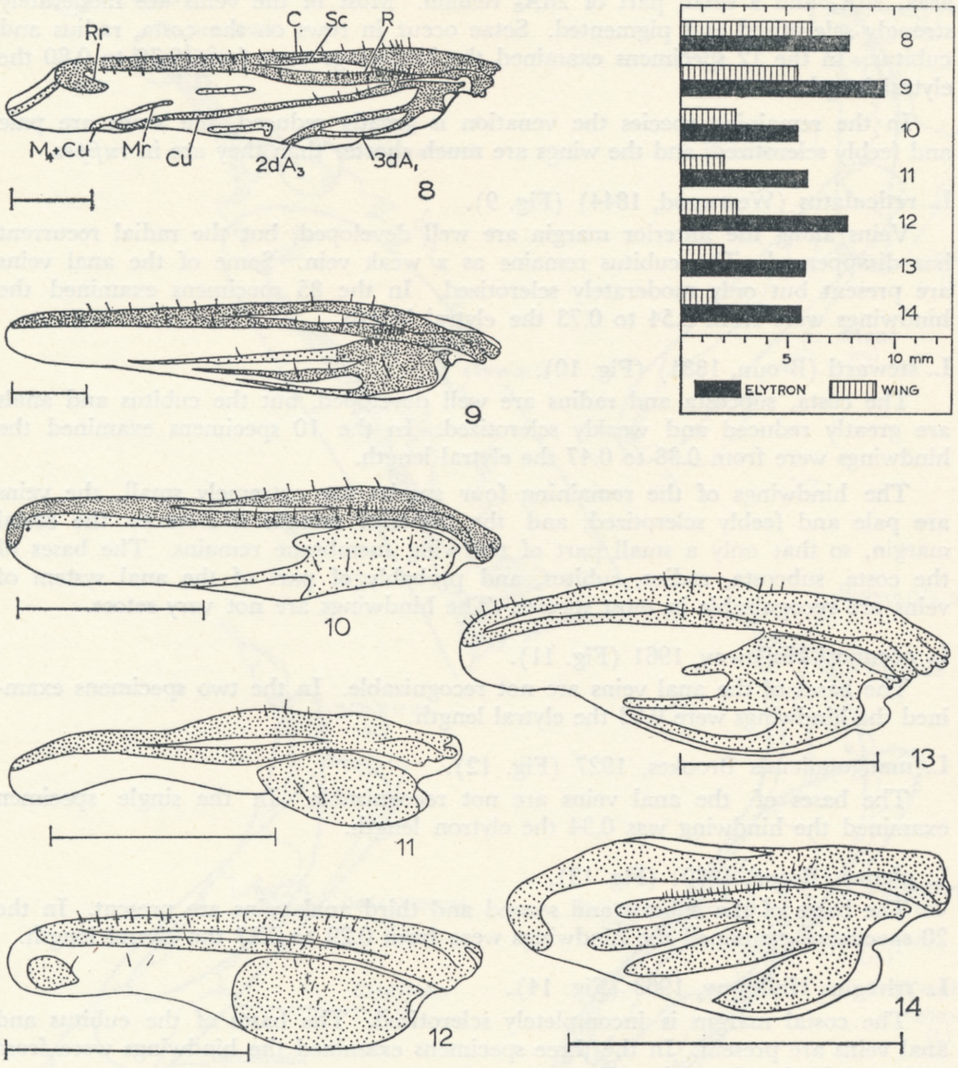
In the 14 specimens examined the hindwings were from 0.26 to 0.33 the elytral length.

Genus LISSOTES Westwood, 1855

The seven New Zealand species referred to this genus (Holloway, 1961, 1963) and the Australian species that I have examined, *L. curvicornis* (Boisd., 1835), *L. cancroides* (Fab., 1787), *L. furcicornis* Westwood, 1871, *L. darlingtoni* Benesh, 1943, *L. menalcas* Westwood, 1855, all have vestigial hindwings. In the New Zealand species-group the extent to which the hindwings have been reduced differs a great deal from one species to the next. The relationship of hindwing length to elytron length in each of the specimens illustrated is shown in the histogram beside Fig. 8, and the infraspecific variation in this is given below.

L. rufipes Sharp, 1886 (Fig. 8).

The costa, subcosta and radius are well developed and the radial recurrent and a small section of the apical part of the wing are present. The posterior margin of the wing has moved towards the costal margin, but the cubitus and medial



FIGS. 8–14.—Vestigial hindwings of New Zealand species of *Lissotes*. (8) *L. rufipes* ♀ (Nelson); (9) *L. reticulatus* ♀ (Wellington); (10) *L. stewarti* ♂ (Whangarei); (11) *L. oconnori* ♂ (Spirits Bay); (12) *L. mangonuiensis* ♂ (Mangonui); 13 *L. planus* ♂ (Waipoua Forest); (14) *L. triregius* ♀ (Three Kings Is.).

Histogram shows relationship of hindwing length to elytron length in each of the specimens illustrated (Figs. 8–14). (Scales beside figures equal 1.0mm.) Abbreviations: 2dA$_3$, 3dA$_1$, branches of second and third anal veins; C, costa; Cu, cubitus; M$_4$, branch of media; Mr, medial recurrent; R, radius; Rr, radial recurrent; Sc, subcosta. Axillary sclerites not shown. Basal edge of anal area is folded under in all figs. Close stipple indicates moderate pigmentation; sparse stipple indicates weak pigmentation; clear areas indicate wing membrane.

recurrent are recognisable, and a small part of $M_4 + Cu$ remains. In the anal area, $3dA_1$ and a small part of $2dA_3$ remain. Most of the veins are moderately strongly sclerotized and pigmented. Setae occur in rows on the costa, radius and cubitus. In the 12 specimens examined the hindwings were from 0.78 to 0.80 the elytral length.

In the remaining species the venation is greatly reduced, the veins are pale and feebly sclerotized, and the wings are much shorter than they are in *rufipes*.

L. reticulatus (Westwood, 1844) (Fig. 9).

Veins along the anterior margin are well developed, but the radial recurrent has disappeared. The cubitus remains as a weak vein. Some of the anal veins are present but only moderately sclerotized. In the 85 specimens examined the hindwings were from 0.54 to 0.73 the elytral length.

L. stewarti (Broun, 1881) (Fig. 10).

The costa, subcosta and radius are well developed, but the cubitus and anals are greatly reduced and weakly sclerotized. In the 10 specimens examined the hindwings were from 0.38 to 0.47 the elytral length.

The hindwings of the remaining four species are extremely small, the veins are pale and feebly sclerotized, and the posterior margin is close to the costal margin, so that only a small part of the wing membrane remains. The bases of the costa, subcosta, radius, cubitus, and probably of part of the anal system of veins are recognizable in most species. The hindwings are not very setose.

L. oconnori Holloway, 1961 (Fig. 11).

The bases of the anal veins are not recognizable. In the two specimens examined the hindwings were 0.33 the elytral length.

L. mangonuiensis Brookes, 1927 (Fig. 12).

The bases of the anal veins are not recognizable. In the single specimen examined the hindwing was 0.34 the elytron length.

L. planus (Broun, 1880) (Fig. 13).

The bases of the cubitus and second and third anal veins are present. In the 20 specimens examined the hindwings were from 0.29 to 0.37 the elytral length.

L. triregius Holloway, 1963 (Fig. 14).

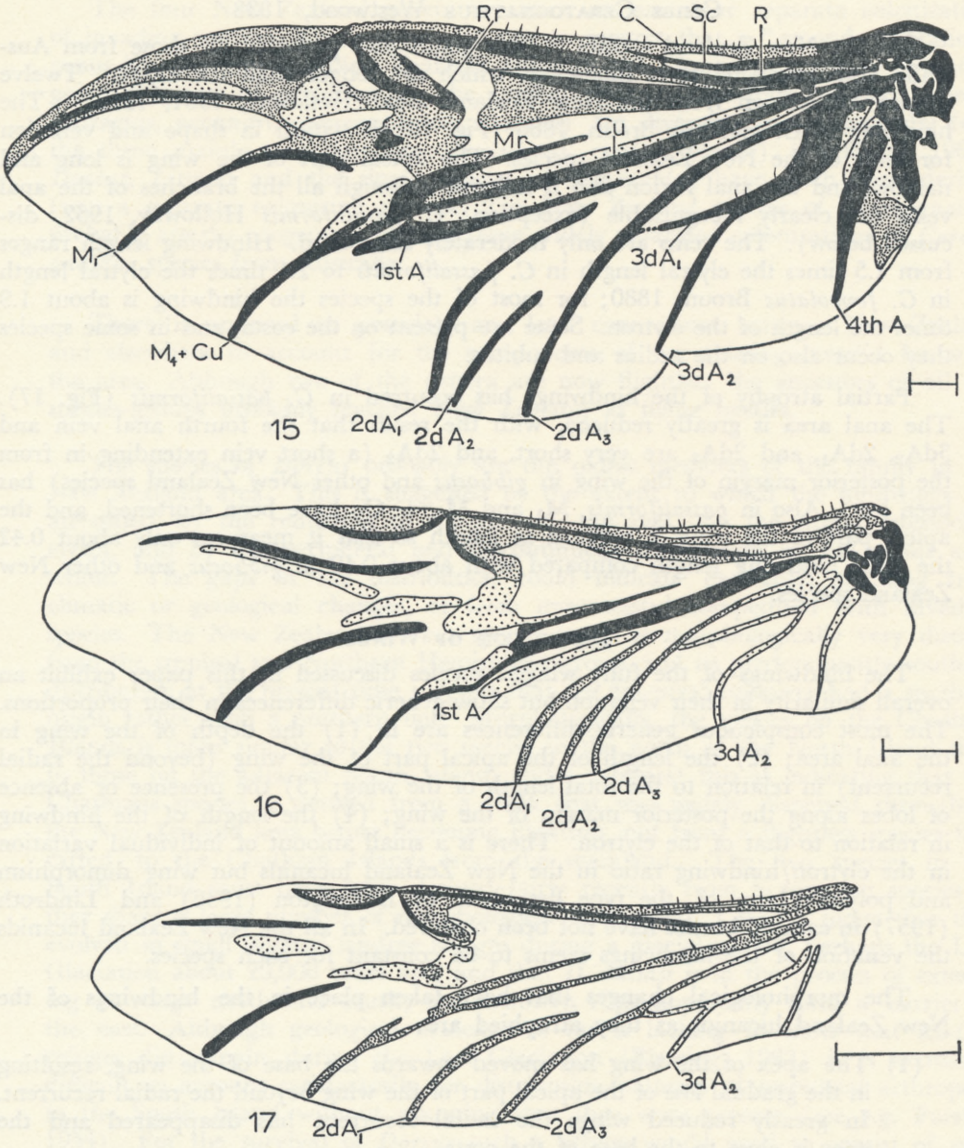
The costal margin is incompletely sclerotized. The bases of the cubitus and anal veins are present. In the three specimens examined the hindwings were from 0.18 to 0.26 the elytral length.

Genus DENDROBLAX White, 1846

This genus is monotypic and known only from New Zealand.

D. earlii White, 1846 (Fig. 15).

Westwood (1855) stated that females of this species are apterous, but in all the specimens I have examined (19 males, 40 females) the hindwings are strongly developed and about 1.6 times the elytral length. All the veins are strongly sclerotized and deeply pigmented. The posterior margin of the wing is notched near $3dA_2$, and beyond the notch the wing is very broad. The radial recurrent is very conspicuous. A few short setae are present along the costal margin and on the third anal vein. The apical part of the wing is about 0.4 times the total wing length.



FIGS. 15–17.—Flying wings of *Dendroblax* and *Ceratognathus*. (15) *D. earlii* ♂ (Levin); (16) *C. gibbosus* ♂ (Upper Hutt); (17) *C. passaliformis* ♂ (Wellington). (Scales beside figures equal 1.0mm.)

Abbreviations: 1stA, 4thA, first and fourth anal veins; $2dA_1$, $2dA_2$, $2dA_3$, branches of second anal vein; $3dA_1$, $3dA_2$, branches of third anal vein; C, costa; Cu, cubitus; M_1, M_4, branches of media; Mr, medial recurrent; R, radius; Rr, radial recurrent; Sc, subcosta. Axillary sclerites not shown in Fig. 17. Black indicates deep pigmentation; close stipple indicates moderate pigmentation; sparse stipple indicates weak pigmentation; clear areas indicate wing membrane.

Genus Ceratognathus Westwood, 1838

All the New Zealand species of this genus and probably all those from Australia and Tasmania have hindwings which are longer than the elytra. Twelve species are known from the New Zealand area (Holloway, 1961, 1962). The hindwing of *C. gibbosus* Broun, 1886 (Fig. 16) is typical in shape and venation for most of the New Zealand species. The apical part of the wing is long and narrow, and the anal region also is narrow, although all the branches of the anal veins are clearly recognizable (exception: *C. passaliformis* Holloway, 1962, discussed below). The veins are only moderately sclerotized. Hindwing length ranges from 1.5 times the elytral length in *C. passaliformis* to 2.1 times the elytral length in *C. foveolatus* Broun, 1880; for most of the species the hindwing is about 1.9 times the length of the elytron. Setae are present on the costa, and in some species they occur also on the radius and cubitus.

Partial atrophy of the hindwings has occurred in *C. passaliformis* (Fig. 17). The anal area is greatly reduced, with the result that the fourth anal vein and $3dA_2$, $2dA_1$, and $2dA_3$ are very short, and $2dA_2$ (a short vein extending in from the posterior margin of the wing in *gibbosus* and other New Zealand species) has been lost. Also in *passaliformis,* M_1 and $M_4 + Cu$ have been shortened, and the apical part of the wing is reduced in length so that it measures only about 0.42 the total hindwing length compared with about 0.49 in *gibbosus* and other New Zealand species.

Discussion of Wings

The hindwings of the fully winged species discussed in this paper exhibit an overall similarity in their venation but show generic differences in their proportions. The most conspicuous generic differences are in (1) the depth of the wing in the anal area; (2) the length of the apical part of the wing (beyond the radial recurrent) in relation to the total length of the wing; (3) the presence or absence of lobes along the posterior margin of the wing; (4) the length of the hindwing in relation to that of the elytron. There is a small amount of individual variation in the elytron/hindwing ratio in the New Zealand lucanids but wing dimorphism and polymorphism of the type described by Darlington (1936) and Lindroth (1957) in carabid beetles have not been observed. In all the New Zealand lucanids the venation of the hindwings seems to be constant for each species.

The morphological changes that have taken place in the hindwings of the New Zealand lucanids as they atrophied are:

(1) The apex of the wing has moved towards the base of the wing, resulting in the gradual loss of the apical part of the wing beyond the radial recurrent. In greatly reduced wings the radial recurrent has disappeared and the apex is close to the base of the costa.

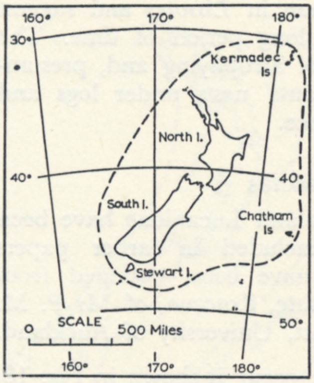
(2) The posterior margin of the wing has moved towards the costal margin. This results in a shortening of the branches of the anal veins, and of the cubitus and media. In greatly atrophied wings the media disappears completely and only the bases of the cubitus and anals are recognizable.

(3) There is an overall decrease in the size of the wing.

(4) The pigmentation and sclerotization of the veins are reduced.

(5) In some species the setae increase in length and number on various parts of the wing.

The illustrations of the wings of *L. rufipes* (Fig. 8) and *C. passaliformis* (Fig. 17) clearly show that these changes do not take place strictly in the order given



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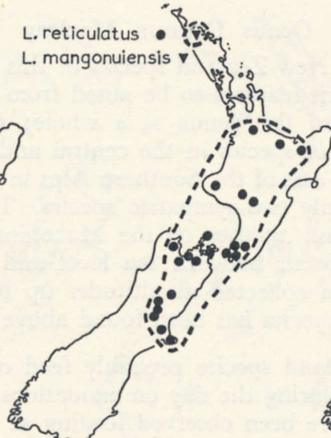

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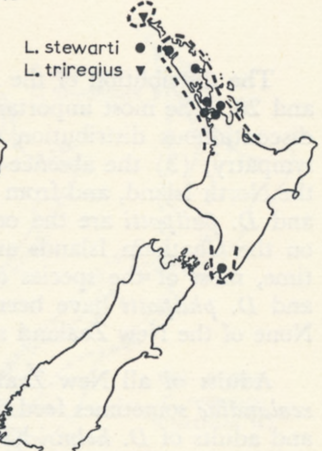

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Fig. 18.—Map of New Zealand and adjacent islands. Broken line encloses area in which Lucanidae occur.

Figs. 19–23.—Maps showing distribution of flightless Lucanidae in the New Zealand area. (19) and (20) *Dorcus* species; (21)–(23) *Lissotes* species. Symbols indicate areas in which the species occur, not necessarily single specimens.

above; rather they tend to be taking place simultaneously within a species. The rates and extent of wing atrophy can vary markedly within a group of related species (see Figs. 2–7, 8–14). The morphological changes listed above are similar to those occurring in atrophied wings of carabid beetles (Darlington, 1936).

The atrophied wings of one species of *Lissotes* contain an almost complete set of veins (see *L. rufipes,* Fig. 8); the colonizing ancestor of the *Lissotes* group must have had hindwings that were at least as well developed as those of *L. rufipes,* and I would judge that it reached New Zealand as a flying species. Similarly, since the atrophied hindwings of *D. novaezealandiae* (Fig. 2) have retained many of the veins that occur in fully winged species the ancestral species of the *Dorcus* group probably arrived in New Zealand as a flying beetle. The New Zealand species of *Lissotes* and *Dorcus* have small eyes, and elytra that interlock firmly along the elytral suture. These features, which often are correlated with flightlessness in beetles, are more pronounced in *Dorcus* than in *Lissotes* and suggest that the *Dorcus* group has been flightless for a very long period of time. The wings of *C. passaliformis* are in the very early stages of atrophying and, presumably, still could be functional. This species lives in ants' nests under logs and seems to be specially adapted to a subterranean existence.

DISTRIBUTION OF GENERA AND SPECIES

The data for the distribution maps of the New Zealand Lucanidae have been gathered mainly from distributional lists that were included in earlier papers (Holloway, 1961, 1962, 1963). Additional records have been obtained from material in the collections of the Forest Research Institute, Rotorua, of Mr P. M. Johns, University of Canterbury, and of Mr J. C. Watt, University of Auckland.

The area within which the New Zealand Lucanidae occur is shown in Fig. 18. To date, lucanids have not been collected from south of Stewart Island in the New Zealand region, but the family is able to extend its range south of latitude 47° S. in Chile (Kuschel, pers. comm.).

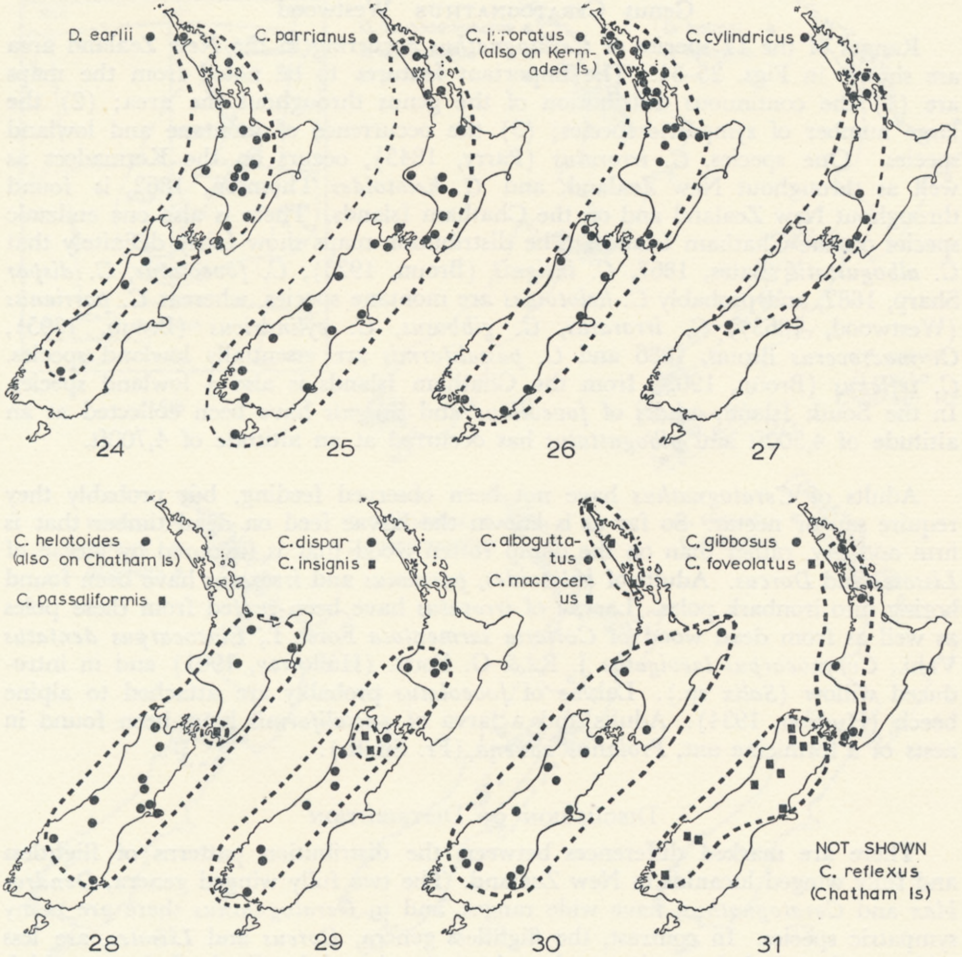
Genus DORCUS Macleay

The distribution of the New Zealand species of this genus is shown in Figs. 19 and 20. The most important features to be noted from the maps are (1) the very discontinuous distribution of the genus as a whole; (2) the small amount of sympatry; (3) the absence of species in the central and extreme northern parts of the North Island, and from east of the Southern Alps in the South Island. *D. helmsi* and *D. philpotti* are the only two sympatric species. There is an endemic species on the Chatham Islands and another on the Mokohinau Islands. At the present time, most of the species occur between sea level and 2,000 feet, but *D. helmsi* and *D. philpotti* have been collected at altitudes up to 4,000 feet in Southland. None of the New Zealand species has been found above the timber line.

Adults of all New Zealand species probably feed on sap; those of *D. novaezealandiae* sometimes feed during the day on exudations under bark of *Nothofagus,* and adults of *D. helmsi* have been observed feeding at night on sap exuding from trunks of broad-leaved trees (Holloway, 1961). The larvae have been found in rotting wood and soil, and in general seem not to be attached to any particular species of plant; larvae of *D. novaezealandiae* often are abundant among humus and fibrous roots of ferns at the bases of *Nothofagus* trunks, and they also occur in rotting wood of *Dacrydium cupressinum* Lamb. and *Podocarpus spicatus* Mirbel. Mr R. G. Ordish of the Dominion Museum, has collected larvae of *D. helmsi* several inches below the surface in a garden on Stewart Island, and the gut content of these specimens consists mainly of soil with scarcely any recognizable fragments of plant material.

Genus LISSOTES Westwood

The distribution of the New Zealand species of *Lissotes* is shown in Figs. 21–23. The important features to be noted from the maps are (1) the continuous distribution of the genus in the North Island and in part of the South Island; (2) the relatively large number of sympatric species, compared with *Dorcus*; (3) the absence of the genus from western and southern parts of the South Island. *Lissotes* is not represented on the Chatham Islands. Most of the species occur between sea level and about 2,000 feet, but *L. rufipes* and *L. reticulatus* have been found at altitudes up to 3,000 feet. No species are known from above the timber line.



Figs. 24–31.—Maps showing distribution of fully winged Lucanidae in the New Zealand area. (24) *Dendroblax earlii*; (25)–(31) *Ceratognathus* species. Symbols indicate areas in which the species occur, not necessarily single specimens.

The food and shelter requirements of all stages of *Lissotes* seem to be similar to those of *Dorcus*, and in the Wellington District larvae, pupae and adults of *D. novaezealandiae* and *L. reticulatus* occur together in the same rotten logs.

Genus Dendroblax White

The distribution of the single species of *Dendroblax* is shown in Fig. 24. To date, no specimens have been collected in the east and extreme south of the South Island or on the Chatham Islands, but the species is otherwise widespread throughout New Zealand. Although most of the specimens have been found near sea level, some have been collected on the central plateau of the North Island and on Ben Lomond in the South Island, but the exact altitudes at which these specimens were taken are not known.

The ecological requirements of *D. earlii* are very imperfectly known. It is thought that the larvae feed on roots (Holloway, 1961).

Genus CERATOGNATHUS Westwood

Ranges of the 12 species of *Ceratognathus* occurring in the New Zealand area are shown in Figs. 25–31. The important features to be noted from the maps are (1) the continuous distribution of the genus throughout the area; (2) the large number of sympatric species; (3) the occurrence of montane and lowland species. One species, *C. irroratus* (Parry, 1845), occurs on the Kermadecs as well as throughout New Zealand, and *C. helotoides* Thomson, 1862, is found throughout New Zealand and on the Chatham Islands. There is also one endemic species on the Chatham Islands. The distribution maps show fairly definitely that *C. alboguttatus* Bates, 1867, *C. insignis* (Broun, 1923), *C. foveolatus, C. dispar* Sharp, 1882, and probably *C. helotoides* are montane species, whereas *C. parrianus* (Westwood, 1863), *C. irroratus, C. gibbosus, C. cylindricus* (Broun, 1895), *C. macrocerus* Broun, 1886 and *C. passaliformis* are essentially lowland species. *C. reflexus* (Broun, 1909) from the Chatham Islands is also a lowland species. In the South Island, adults of *foveolatus* and *insignis* have been collected at an altitude of 4,300ft and *alboguttatus* has occurred at an altitude of 4,700ft.

Adults of *Ceratognathus* have not been observed feeding, but probably they require sap or nectar. So far as is known the larvae feed on dead timber that is firm and dry, rather than on the damp rotten wood that is favoured by larvae of *Lissotes* and *Dorcus*. Adults of *helotoides, parrianus* and *irroratus* have been found boring into ironbark poles. Larvae of *irroratus* have been reared from these poles as well as from dead wood of *Coriaria sarmentosa* Forst. f., *Elaeocarpus dentatus* Vahl., *Corynocarpus laevigatus* J. R. & G. Forst. (Holloway, 1961) and in introduced willow (*Salix* sp.). Larvae of *foveolatus* probably are attached to alpine beech (Hudson, 1934). Adults and a larva of *passaliformis* have been found in nests of a formicine ant, *Prolasius advena* (Fr. Smith).

DISCUSSION OF DISTRIBUTION

There are marked differences between the distribution patterns of flightless and fully winged lucanids in New Zealand. The two fully winged genera, *Dendroblax* and *Ceratognathus,* have wide ranges, and in *Ceratognathus* there are many sympatric species. In contrast, the flightless genera, *Dorcus* and *Lissotes,* are less widespread and their species tend to be isolated and localized. I do not think that the discontinuous ranges of these two genera can be accounted for entirely by inadequate collecting as other lucanid material has been collected from the gaps. The southern part of the North Island is the only region in which *Dorcus* and *Lissotes* are known to occur together; elsewhere the two genera are strictly allopatric. Although some of the flightless species occur at altitudes up to 4,000ft they are more characteristic of lowland areas, and temperature may play a very important role in limiting their distribution. Several of the fully winged species have montane rather than lowland ranges; in some instances their larvae probably are attached to alpine beeches, although beeches are absent from Mount Egmont where adults of several species have occurred.

HISTORY OF THE LUCANIDAE IN NEW ZEALAND

The earliest known fossil lucanid from anywhere in the world is preserved in Baltic Amber of Oligocene age (Waga, 1883). Unfortunately, to date no fossil lucanids have been found in New Zealand, so attempts at interpreting the history and evolution of the family in the New Zealand region have to be based on indirect evidence obtained from studies of the living species and from the geological record.

The four New Zealand genera represent at least four separate colonizations of invading species. There is no evidence to suggest that a " second generation " genus has developed in New Zealand, although the *Lissotes* group may be undergoing this sort of evolution at the present time as the four northern species (*triregius, oconnori, mangonuiensis, stewarti*) are diverging morphologically from the three mainly southern ones (*reticulatus, rufipes, planus*) (Holloway, 1963). *Dorcus, Lissotes* and the single species of *Dendroblax* have each been derived from a separate colonizing species. The New Zealand species of *Ceratognathus* probably are the progeny of at least three widely separated colonizations of *Ceratognathus* species from Australia.

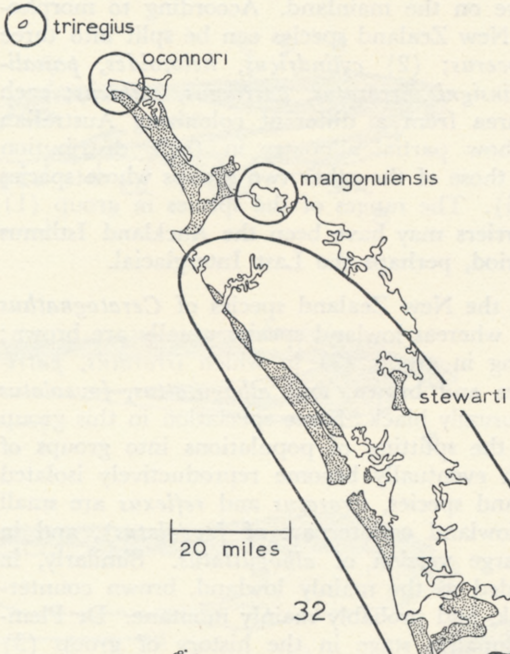
There is no need to postulate any land connections between New Zealand and elsewhere to account for the components of the existing lucanid fauna of the area. Although two of the genera are now flightless the ancestors of all the species-groups probably reached New Zealand as flying beetles.

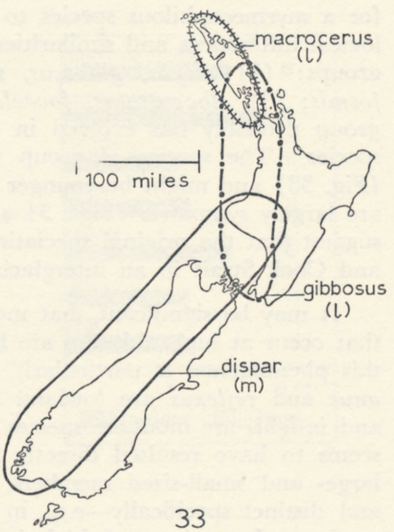
The species of *Dorcus* probably are the oldest members of the family in the New Zealand area. This is suggested by the extent to which the hindwings are atrophied, by the reduction in the size of the eyes, by the firmly interlocked elytra, and by the peripheral and discontinuous distribution of the genus as a whole. The gaps in the distribution could indicate extinction resulting from climatic or geological changes, or from unsuccessful competition with invading species. The New Zealand *Dorcus* species-group is morphologically very distinct from the tropical and Northern Hemisphere group, and its predominantly southern distribution at the present time suggests that the ancestral colonizer had a southern origin rather than a northern one. Morphologically, the species on the Chatham Islands is more similar to the two species in the north of the North Island than to those on the adjacent South Island, and I interpret this as indicating that the Chathams species is derived from a stock that was widely dispersed throughout the New Zealand area before becoming flightless, not from a flightless species that rafted to the Chatham Islands from the mainland. The two species in the South Island must have been derived fairly recently from a common species as they share a large number of morphological characters. I would judge that they evolved in small isolated ice-free refuges during a glacial period, perhaps the Last Glaciation about 20,000 years ago, and that *D. helmsi* is in the process of extending its range north and south; the Southern Alps apparently form a barrier to the east. Although geological evidence so far is lacking to show that ice-free refuges did remain during the Last Glaciation (Fleming, 1962) it is extremely difficult to account satisfactorily for distribution patterns of terrestrial arthropods in the South Island without assuming that they were present (see e.g. Forster, 1954). For the survival of *Dorcus* such a refuge would need to consist of only scrubby coastal vegetation, or perhaps even just peaty soil, and as several extant species can tolerate cold wet conditions for most of the year it seems reasonable to assume that these or other species of the genus could have survived during glacial periods. If the New Zealand species-group of *Dorcus* is older than the *Lissotes* group then almost certainly it dates back beyond the Last Interglacial (about 70,000 to 150,000 years ago) and perhaps beyond the Pleistocene.

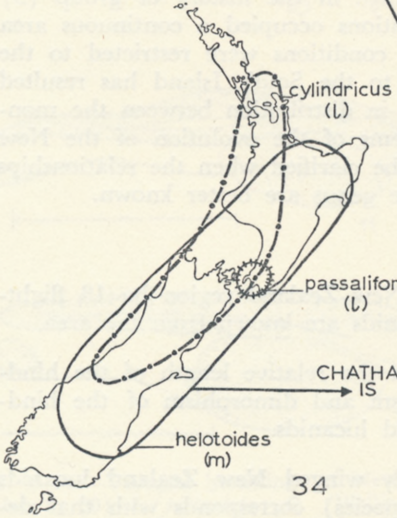
The seven New Zealand species referred at the present time to *Lissotes* differ markedly in a number of morphological characters from the Australian species of this genus, and may eventually be placed in a genus of their own. In the extent of wing atrophy, reduction in size of the eyes, and interlocking of the elytra along the suture, the New Zealand *Lissotes* has less of the appearance of a relict group than has the New Zealand *Dorcus.* Also, the distribution of *Lissotes* is much more continuous than that of *Dorcus.* Its absence from western and southern parts of the South Island and from Stewart Island may indicate that the group is of tropical origin and cannot tolerate a cold, wet climate or that it became extinct in these regions during a glacial period and has not yet recolonized them. Four localized but closely related species of *Lissotes* (*triregius, oconnori, mangonuiensis* and *stewarti*) occur in the Far North of New Zealand (see Fig. 32), and their formation seems to have resulted from isolation on islands in post-Miocene times of a formerly more widespread but flightless stock. Fleming (1962) shows the Far North as a group of islands during the Pliocene, and he has informed me (oral comm.) that the areas of sand now linking these islands are so low that they probably were covered by high level seas of interglacial intervals, including the Last Interglacial about 70,000 to 150,000 years ago. A comparison of these former (post-Miocene) barriers and the range of *Lissotes* in the Far North indicates that the origins of the northern species can be traced back at least to the Last Interglacial (see Fig. 32). The species on the Three Kings (*triregius*) may have been isolated during the Pliocene as this group of islands has been separated from the mainland by very deep seas since that time, and as *triregius* is no more distinct morphologically than *oconnori, mangonuiensis* and *stewarti* it is very likely that all four species date back more than 2,000,000 years. If so, their failure to spread into each others' range may be due to the unsatisfactory habitat of the dune-sand areas that link the old islands. The remaining three species of *Lissotes* (*planus, reticulatus* and *rufipes*) appear to have evolved from a southern stock that probably was separated from the northern stock by post-Miocene seas in the vicinity of the Auckland Isthmus. The spread northwards of *planus* and southwards of *stewarti* may have occurred in fairly recent times. *L. rufipes* has a very localized range in the South Island and could have evolved in a refuge in the Nelson District (? during the Last Glaciation). Morphologically (except for the hindwings) this species is very similar to *reticulatus* which occurs in both the North and South Islands as well as on islands in Cook Strait. *L. reticulatus* has probably extended its range very recently, perhaps while sea level was still low at the end of the Last Glaciation some 15,000 years ago, as North Island populations seem to be identical with those of the South Island. The Southern Alps no doubt are acting as a barrier in the westward spread of this species in the South Island.

Dendroblax, with a single highly variable species occurring throughout most of New Zealand at the present time, is related to *Streptocerus* Fairmaire, 1850, from Chile and to *Lamprima* Latreille, 1806 and *Phalacrognathus* Macleay, 1885 from Australia, New Guinea and Lord Howe Island. It is the only genus of this group in which sexual dimorphism is not apparent. Whether this absence of dimorphism is due to specialization or lack of specialization is not clear at the present time. *D. earlii* could be an old, plastic species rather than a recent invader as it is very distinct from its geographically nearest relatives.

The genus *Ceratognathus* occurs in Australia and Tasmania as well as in New Zealand. A large amount of speciation has taken place in this genus in New Zealand, and some of the species are morphologically very close to Australian species. It appears that basic *generic* characters of the group are very stable, but that "trivial" specific changes—e.g., allometric differences in the mandibles, and minor changes in the shapes of parameres of the male genitalia, have become fixed very rapidly in some populations. The genus has been in the New Zealand area long enough for an endemic species to evolve on the Chatham Islands, and







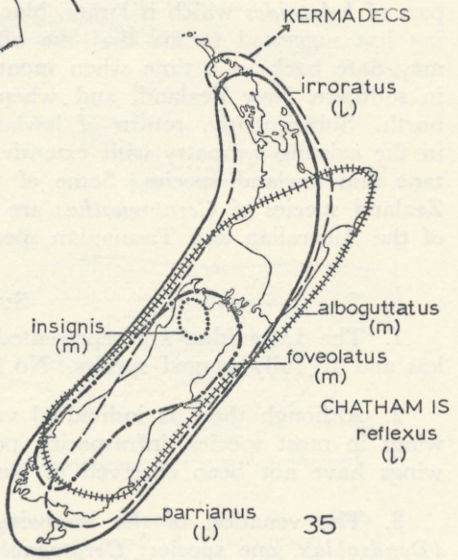


Fig. 32.—Map showing ranges of the four northern species of *Lissotes* and their relationship to former geographic barriers. Former marine barriers are shown in low areas of post-Miocene sediments (stippled) (from Geological Map of N.Z., D.S.I.R., in press, 1958).

Fig. 33.—Map showing ranges of three closely related species of *Ceratognathus*. The partial sympatry of the species suggests a former allopatry, with the original barriers at the Auckland Isthmus and Cook Strait in an interglacial period.

Fig. 34.—Map showing ranges of three closely related, sympatric species of *Ceratognathus*. The pattern and history of speciation is not apparent.

Fig. 35.—Map showing ranges of five mainland (and one Chatham Is. sp.) species of *Ceratognathus*, all closely related, and all sympatric. The pattern and history of speciation does not show, unless it be altitudinal. Abbreviations: 1, lowland species; m, montane species.

for a myrmecophilous species to evolve on the mainland. According to morphological differences and similarities the New Zealand species can be split into three groups: (1) *dispar, gibbosus, macrocerus*; (2) *cylindricus, helotoides, passaliformis*; (3) *alboguttatus, foveolatus, insignis, irroratus, parrianus, reflexus*; each group probably has evolved in the area from a different colonizing Australian species. The species of group (1) show partial allopatry in their distribution (Fig. 33) and might be younger than those of the other two groups whose species are largely sympatric (Figs. 34 and 35). The ranges of the species in group (1) suggest that the original speciation barriers may have been the Auckland Isthmus and Cook Strait in an interglacial period, perhaps the Last Interglacial.

It may be significant that most of the New Zealand species of *Ceratognathus* that occur at high altitudes are black, whereas lowland species usually are brown; this phenomenon is particularly striking in group (3) in which *irroratus, parrianus* and *reflexus* are lowland species and brown, and *albogutattus, foveolatus* and *insignis* are montane species and usually black. Some speciation in this group seems to have resulted directly from the splitting of populations into groups of large- and small-sized members which eventually become reproductively isolated and distinct specifically—e.g., in lowland species, *irroratus* and *reflexus* are small versions of *parrianus* (which is the lowland counterpart of *foveolatus*), and in montane species *foveolatus* is the large version of *alboguttatus.* Similarly, in group (2), *cylindricus* could be regarded as the mainly lowland, brown counterpart of *helotoides* which is larger, black, and probably mainly montane. Dr Fleming has suggested to me that the allopatric stage in the history of group (3) may date back to a time when montane conditions occupied a continuous area in southern New Zealand, and when lowland conditions were restricted to the north. Subsequently, return of lowland forest to the South Island has resulted in the existing sympatry with extensive overlap in distribution between the montane and lowland species. Some of the problems of the evolution of the New Zealand species of *Ceratognathus* are likely to be clarified when the relationships of the Australian and Tasmanian species of the genus are better known.

Summary

1. The Lucanidae are represented in the New Zealand region by 13 flightless and 13 fully winged species. No fossil lucanids are known from the area.

2. Although there is individual variation in the relative length of the hindwings in most species, infraspecific polymorphism and dimorphism of the hindwings have not been observed in New Zealand lucanids.

3. The venation of the hindwings of fully winged New Zealand lucanids (*Dendroblax*, one species; *Ceratognathus*, 12 species) corresponds with that described previously for the family. The general proportions of the hindwings in fully winged lucanids appear to be characteristic for each genus. Generic differences are most apparent in (1) the depth of the wing in the anal area; (2) the length of the apical part of the wing in relation to that of the remainder of the wing; (3) the presence of lobes along the posterior margin of the wing; (4) the length of the hindwing in relation to the length of the elytron.

4. In flightless species (*Dorcus*, six species; *Lissotes*, seven species) the main morphological changes that have taken place in the hindwings as they have atrophied are: (1) the part of the wing beyond the radial recurrent has been reduced in length or has disappeared completely, and in wings that are greatly reduced the apex is close to the base of the costa; (2) the posterior margin has

moved towards the costal margin; (3) there has been a general overall decrease in the size of the wing.

5. In flightless species the eyes are small and the elytra interlock firmly.

6. The atrophied wings of the New Zealand species-group of *Dorcus* and of *Lissotes* are reduced to different extents in different species. Probably the ancestral species of each group arrived in New Zealand as a flying beetle.

7. The hindwings in one species of *Ceratognathus* (*C. passaliformis*) are beginning to atrophy.

8. There are vast differences between distribution patterns of flightless and fully winged lucanids in New Zealand. Flightless species tend to be allopatric and to have restricted ranges; they occur almost exclusively in lowland areas. Fully winged species usually have wide, overlapping ranges, and some are restricted to montane regions.

9. Adults of all species probably feed on sap and are unspecific in their choice of food plants. Larvae of flightless species complete their development in rotten wood or soil; those of *Dendroblax* probably eat roots; those of *Ceratognathus* feed on sound, dead wood and some species probably are attached to specific host plants.

10. *Dorcus, Lissotes* and *Dendroblax* have evolved in New Zealand from separate colonizing invaders. The New Zealand species of *Ceratognathus* seem to be the progeny of at least three species that arrived from Australia or Tasmania at widely separated times. No secondary genera of Lucanidae have evolved yet in the New Zealand area.

11. Speciation in the flightless genera seems to have resulted mainly from isolation of flightless populations on islands and in ice-free refuges. Some speciation in the New Zealand *Ceratognathus* group has resulted directly from colonization of at least three Australian or Tasmanian species; the progeny of these have split into montane and lowland species, and into large- and small-sized species which are morphologically very similar.

12. Some of the existing species of *Lissotes* probably began evolving as long ago as the Pliocene (more than 2,000,000 years ago) and no later than the Last Interglacial (70,000 to 150,000 years ago) from a flightless stock that became isolated on islands.

13. The *Dorcus* species-group probably has been in the New Zealand area longer than the *Lissotes* group.

14. *Dendroblax earlii* seems to be an old plastic species in New Zealand, rather than a recent arrival.

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