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New Zealand Cave Fauna. II—The Limestone Caves Between Port Waikato and Piopio Districts

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Abstract

A survey was made of fauna occurring in limestone caves of the North Island between Port Waikato, south of Waikato Heads, and Piopio, just north of Mokau River. Methods of collection are described. A catalogue of species is given; approximately 6% of these are considered to be troglobites; 43% troglophiles; 23% trogloxenes (tolerant) and 29% trogloxenes (intolerant). Troglobites occurred among Collembola and Coleoptera (Fam.: Carabidae). Beetles of the genera *Duvaliomimus* and *Neanops* (Sub-fam.: Trechinae) exhibited regressive modifications. Theories of regressive evolution are reviewed and their application to New Zealand species discussed. It is thought that troglobic Coleoptera became isolated in caves during the hot, dry interglacial stage of the lower Pleistocene, nearly two million years ago. Global affinities of the cave fauna are considered.

INTRODUCTION

LIMESTONE outcrops in the North Island (Fig. 1) follow a course roughly parallel with the West Coast. Caves are known at Kawakawa, Whangarei and Waipu in the North; south of the Waikato Heads in the Port Waikato area; in the country west from Huntly; at Karamu, near Mt Pirongia, and in the Kawhia district. Beyond Kawhia is a large area extending south to the Mokau River, which is overlain by the Te Kuiti limestone formation. The country here is pitted with tomos.* Much of the drainage is underground and there are very many caves, both large and small.

On the eastern side of the Island there is also a chain of limestone outcrops from northern Hawke's Bay to Castle Point, parts of which are covered more or less thickly with volcanic deposits from the Central Plateau. Caves are known, so far, only in the Wairoa and Dannevirke districts.

Work on the collection and identification of New Zealand cave fauna was begun by the author in 1956. It has not yet been possible to explore caves in all areas and the scope of this paper is limited to the limestone country between Port Waikato (lat. 37.20) and Piopio (lat. 38.50) districts, where 36 caves, of widely differing characters, have been searched for specimens. (Fig. 2.)

* *Tomo* is a Maori word meaning sink hole or shaft.

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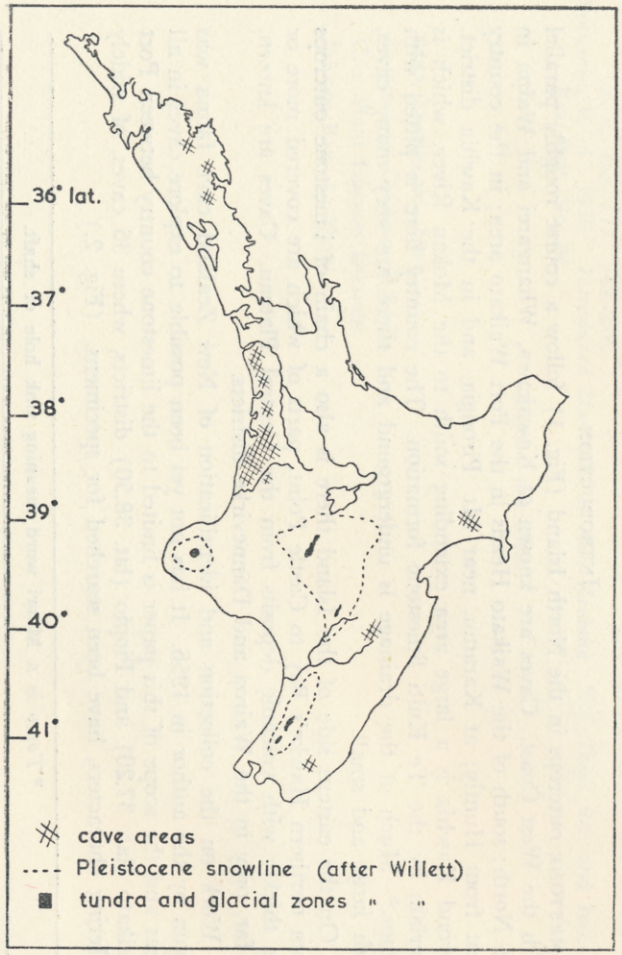


FIG. 1.—Limestone cave areas of the North Island related to the Pleistocene snowline.

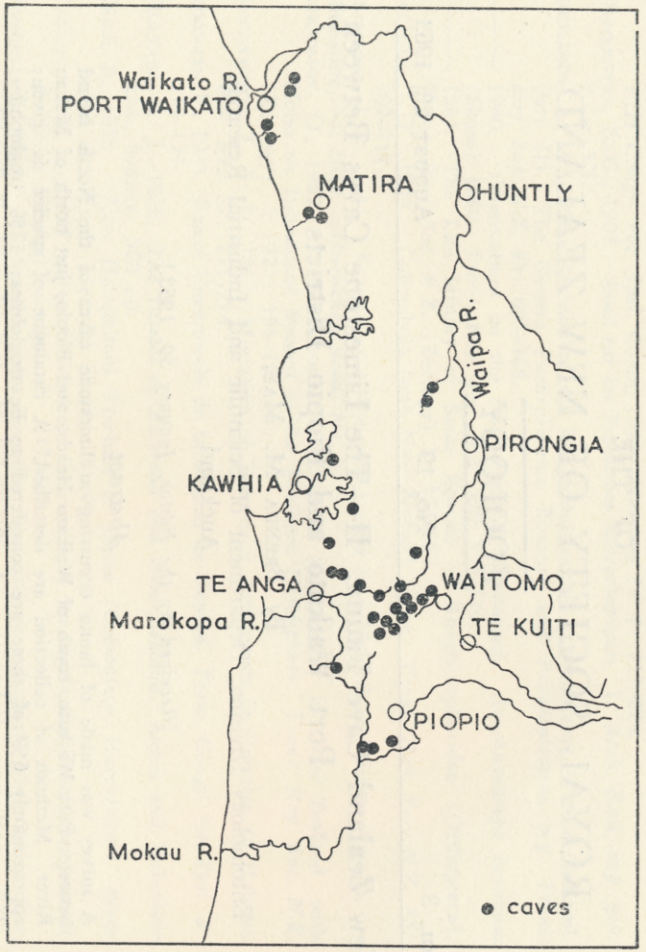


FIG. 2.—Location of caves in the Port Waikato-Piopio area.

Schmidt (1832) described the first known cave beetle, *Leptodirus hohenwarti* (Catopidae: Bathysciinae). Interest in subterranean creatures and hence the study of them can be said to date from that time. Schiner (1854), followed by Racovitza (1907) and Jeannel (1926), erected a classification for cave fauna that is still in use. Since this type of study is comparatively unfamiliar in New Zealand, a brief *resume* is included here.

Cave dwelling animals are placed in three main categories according to their biological relations with the epigean fauna:

1. *Troglobites* (Greek: trogle—cave, bios-life) are obligate cavernicoles, to which conditions of fairly even temperature, darkness and above all high humidity, are essential. They are creatures which live exclusively underground and exhibit modifications that are the result of continuous breeding in this specialised and isolated environment. The degree and form of the modifications differ, but in general they may be summarised as follows: depigmentation; reduction or loss of eyes; loss of wings (in beetles); elongation of mouthparts, limbs and sensory appendages; and, according to recent research, the contraction, sometimes extreme, of the larval stage of the life cycle (Deleurance 1958, 1961).

2. *Troglophiles* (Greek: philos—friend) are facultative cavernicoles; animals indifferent to cave conditions but living there because food is available for them. They may reproduce normally in caves but are equally successful in the bush, in shady cliff hollows or even in damp, man-made tunnels. They are species pre-adapted by their habits and tolerance of humidity.

3. *Trogloxenes* (Greek: xenos—stranger) are in a different physiological category from the foregoing groups. They are creatures of the outside which enter caves for various reasons but do not, as a rule, complete their life cycle there. Some are attracted by dead carcases, some seek coolness in the heat of summer, some are brought in by the stream water while others fall in through holes or are washed in on flood debris. Many of them are doomed to die, due to their inability to accept the new surroundings.

These broad divisions are capable of further dissection, and indeed, Pavan (1958) recognised no less than seven subdivisions, based on the extent to which an animal has chosen the environment, its subsequent capacity for reproduction and hence the possibility of its founding a race of cavernicoles. Such dissection is unwarranted in the present study as the breeding habits of many species are still unknown. A useful purpose may be served, however, by separating the troglox-enes into two groups: (a) *Tolerant*—those which voluntarily enter caves, usually for temporary reasons; (b) *Intolerant*—those which normally avoid caves. In the catalogue of fauna, classification is indicated by the following abbreviations: Tb., troglobite; Tph., troglophile; Tx-t., trogloxene (tolerant); Tx-int., trogloxene (intolerant). Number of yards given indicates distance in cave from nearest known entrance. Identifications of specimens, where not otherwise indicated, were made by the author.

METHODS OF COLLECTION

Collections were made both by hand and with traps based on those used by H. S. Barber (1930) in America. These consist of bait plus a non-repellent pre-servative. The bait used was a pungent mixture of minced raw beef and grated mature cheese kept at about 70deg. F. for 2 weeks; the preservative formula was: Sodium chloride 5gm, potassium nitrate 1gm, chloral hydrate 1gm, dissolved in distilled water to 100cc, plus a few drops of glycerine.

Jam jars were used initially, with preservative in the bottom and a small bait jar hung inside by wire. These gave good results for over a year in Waipuna Cave,

Te Kuiti, but had the disadvantages of being bulky to carry and awkward to empty. Later, 8-dram clip top vials were substituted with a small tube for bait. (Fig. 3.) They proved to be equally effective and much simpler. In both cases the jar was buried to the neck and a stone placed over the top to exclude drops of water and large insects. The $\frac{1}{8}$in gap left for entry was probably an added attraction to small cryptozoic creatures.

On a few occasions, vials with a funnel top, containing meat bait or chopped water cress were sunk in seepage pools to attract aquatic crustaceans, but results were negative. This type of trap must not be left more than 36 hours and was usually taken up the same day. Water nets secured across streams were used for sampling aquatic larvae.

The number and variety of organisms was variable, the limiting factor apparently being lack of moisture. This bears out the findings of Valentine (1930) and Coiffait (1953).

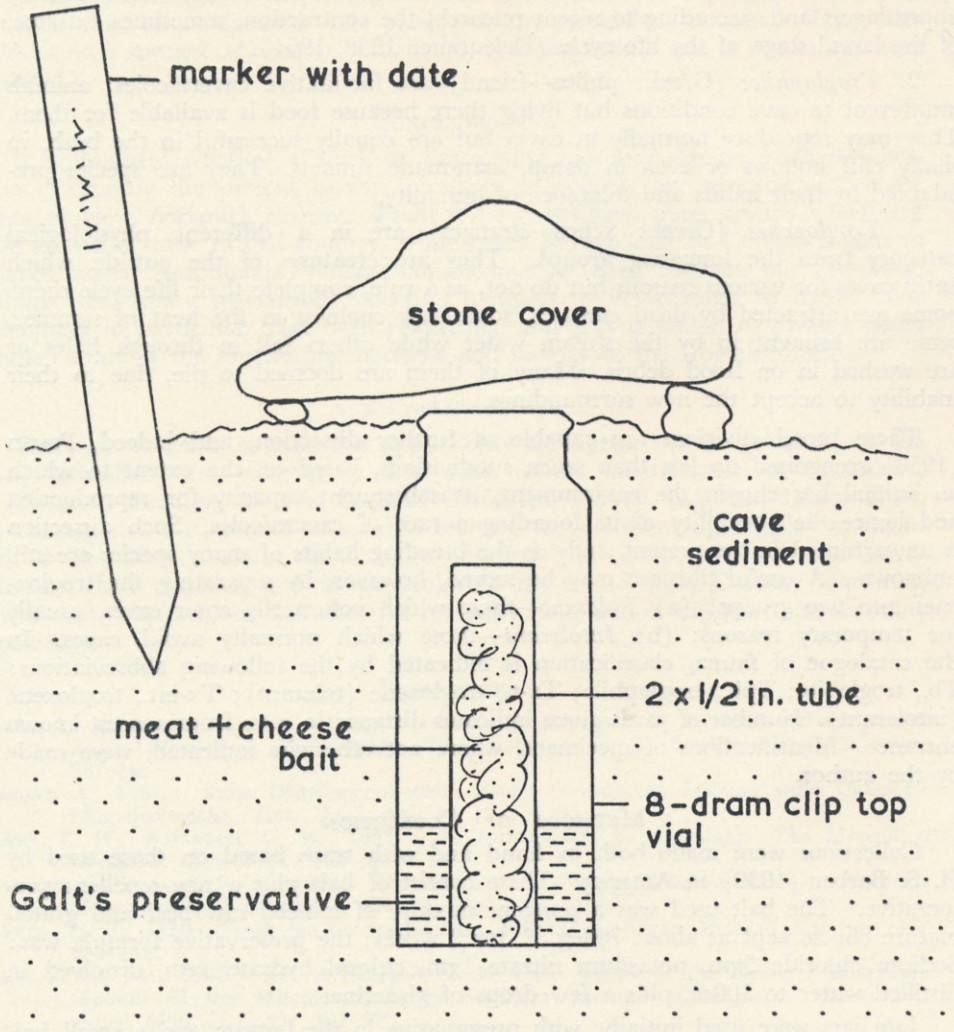


Fig. 3.—Method of trapping terrestrial cave arthropods.

CATALOGUE OF SPECIES

ONYCHOPHORA

Peripatoides novae-zealandiae Hutton Tx-t

Te Kuiti: Waipuna Cave, 50yds, 9.ii.1958, 1 spec. (R. Scott); Ruakuri Cave, 20yds, 30.iii.1959, 1 spec. (L. G. Watson).

Taken during dry periods in summer when cave conditions were more attractive than its normal bush habitat.

CRUSTACEA–ISOPODA

STYLONISCIDAE (det. A. Vandel)

Styloniscus phormianus (Chilton) Tph.

Te Kuiti: Waipuna Cave, on rat droppings, 100yds, 11.i.1958, 1♂, 2♀, partially depigmented, eyes normal (B. M. May); Luckie Strike Cave, ex trap, 150yds, 6.iv.1958, 1 spec. (D. V. May); 500yds, 1♂, 4♀♀ (D. V. May); 150yds, 14.ii.1959, 1♀ totally depigmented, 2 ommatidia only, 1♂, 2♀♀ partially depigmented (B. M. May); 1♂, 1♀ partially depigmented (K. A. J. Wise); Warren's Cave, depth 90ft, 150yds, 20.iv.1959, 1♂ with body totally, eyes partially, depigmented (B. M. May); Virginia Cave, depth 90ft, 150yds, 19.iv.1959, 1♀ partially depigmented (B. M. May).

Port Waikato: Puriri Cave, 350yds, 15.vi.1958, 1 spec. entirely pigmented, eyes normal (B. M. May); 100yds, 1.viii.1959, 4 spec., entirely pigmented (B. M. May).

This terrestrial isopod, which was present in all caves near debris and rat droppings, was described by Chilton (1901) from specimens inhabiting the bases of flax (*Phormium tenax* Forst.) leaves. In dense stands of flax, the microclimate is probably not dissimilar to that of a cave.

AMPHIPODA

GAMMARIDAE (det. D. E. Hurley)

Paraleptamphopus subterraneus (Chilton) Tph.

Port Waikato: Puriri Cave, ex still pool beside stream, 150yds, 1.viii.1959, 5 spec. (B. M. May).

Paracalliope fluviatilis (Thomson) Tph.

Port Waikato: Puriri Cave, ex still pool beside stream, 150yds, 1.viii.1959, 1 spec. (B. M. May).

DECAPODA

ASTACIDAE

Paranephrops planifrons White Tph?

Te Kuiti: Waipuna Cave, ex stream, 300yds, 11.i.1958, 2 spec., colouration pale, eyes normal (R. W. Taylor).

Crayfish were seen frequently in all cave streams. Though noticeably lighter in colour, they were otherwise similar to those living in surface streams.

MYRIAPODA–CHILOPODA

SCOLOPENDRIDAE

Cormocephalus rubriceps (Newport) Tx-t.

Te Kuiti: Waipuna Cave, 40yds, 7.vii.1957, 1 spec. (F. E. Walton).
Piopio: Wairere Falls Cave, 20–50yds, 9.vii.1961, 2 spec. (D. V. May).

DIPLOPODA

IULIDAE (det. O. Schubart)

Ophyiulus verruculiger Verhoeff Tx-int.

Te Kuiti: Virginia Cave, depth 110ft, below entrance, 19.iv.1959, 3♂♂, 5♀♀ (B. M. May).

This is the first record for New Zealand of this introduced Mediterranean species (Schubart, 1962).

METOPIDIOTRICHIDAE

Schedotrigona sp. Tph.

Te Kuiti: Hollow Hill Cave, on wall, 20yds, 3.xi.1957, 2 ♂ ♂ (S. A. Rumsey); 12.i.1958, 2 ♂ ♂ (K. A. J. Wise).

Other species of millipeds have been collected but are not yet identified. At least 5 species are represented.

SYMPHYLA

Members of this group were numerous in some localities but have not yet been identified. They have been taken in association with rat droppings and small animal remains and also in traps with isopods and trechine beetles. They are certainly troglophilic and could well prove to be troglobic.

INSECTA–COLLEMBOLA (det. J. T. Salmon)

HYPOGASTRURIDAE

Tullbergia subantarctica Salmon Tph.

Te Kuiti: Waipuna Cave, 500yds, 18.v.1957, numerous spec. (B. M. May).

Mesaphorura krausbaueri Börner Tph.

Pirongia: Karamu Cave, on rat droppings, 150yds, 21.iv.1957 (B. M. May).
Te Kuiti: Raukuri Cave, 15ft, —.v.1955 (A. M. Richards).

ENTOMOBRYIDAE

Lepidocyrtus cyaneus cinereus Folsom Tph.

Te Kuiti: Waitomo Cave, —.ii.1949 (G. W. Hobbs)

Pseudosinella spelunca Salmon Tb.

Te Kuiti: Waipuna Cave, 600yds, 18.v.1957, Type series (B. M. May).
Te Anga: Taumatatotara, Arch Cavern, on opossum droppings, 50–200yds, 21.x.1961 (B. M. May).

Pseudosinella insoloculata Salmon Tph.

Pirongia: Karamu Cave, on mould-covered rat droppings, 500yds, 21.iv.1957 (B. M. May).

Ceratophysella armata Nic Tph.

Te Kuiti: Waitomo Cave, —.iii.1955 (A. M. Richards); Waipuna Cave, ex trap, 500yds, 31.iii.1957 (F. E. Walton).

ONYCHIURIDAE

Spelaphorura petallata Salmon Tb.

Pirongia: Karamu Cave, on rat droppings, 150yds, 21.iv.1957, Type series (B. M. May).

Onychiurus acicindelius Salmon Tb.

Te Kuiti: Waitomo Cave, —.iii.1955, Type series (A. M. Richards).

Onychiurus novae-zealandiae Salmon Tph.

Te Kuiti: Gardner's Gut Cave, 600yds, on dead rat, 2.vi.1962 (B. M. May).
Te Anga: Taumatatotara, Arch Cavern, on opossum droppings, 50–200yds, 21.x.1961 (B. M. May).

ISOTOMIDAE

Folsomia novae-zealandiae Salmon Tph.

Te Kuiti: Waitomo Cave, 100yds, —.vii.1955 (A. M. Richards).
Pirongia: Tomac Tomo, on rat droppings, 100yds, 20.iv.1957 (B. M. May).

EPHEMEROPTERA (det. K. A. J. Wise)

SIPHLONURIDAE

Ameletopsis perscitus Eaton Tx-int.

Te Kuiti: Waipuna Cave, —.xii.1956, 1 spec. (E. C. Bowater); 100yds, 23.ii.1957, 1 spec. (B. M. May); Hollow Hill Cave, near entrance, 12.i.1958, 1 spec. (K. A. J. Wise); ex stream, 400yds, 15.ii.1959, larva (K. A. J. Wise).

Colorburiscus humeralis (Walk.) Tx-int.

Te Kuiti: Waipuna Cave, near entrance, 11.i.1958, 1 imago, 3 larvae (K. A. J. Wise); Hollow Hill Cave, 25yds, 12.i.1958, 2 spec. (R. W. Taylor); 300yds, 12.i.1958, 2 specs. (K. A. J. Wise); 300yds, 15.ii.1958, 3 specs. (K. A. J. Wise); Luckie Strike Cave, 300yds, ex stream, 14.i.1959, 3 larvae (K. A. J. Wise).

EPHEMERIDAE

Ichthybotus hudsoni (Eaton) Tx-int.

Te Kuiti: Bridal Cave, 50yds, 9.xii.1956, 1 spec. (B. M. May); Hollow Hill Cave, 200yds, 12.i.1958, 3 specs. (B. M. May); 200yds, 12.i.1958, 1 spec. (R. W. Taylor); 300yds, 12.i.1958, 1 spec. (K. A. J. Wise).

LEPTOPHLEBIIDAE

Zephlebia sp. Tx-int.

Te Kuiti: Luckie Strike Cave, 140yds, 14.ii.1959, 1 spec. (K. A. J. Wise); Hollow Hill Cave, 20yds, 15.ii.1959, 2 spec. (B. M. May); 2 specs. (K. A. J. Wise); 300yds, 2 specs. (K. A. J. Wise).

Zephlebia (Zephlebia) dentata (Eaton) Tx-int.

Pirongia: Karamu Cave, 400yds, 17.viii.1957, 1 spec. (B. M. May).
Kawhia: Rubay's Cave, 100yds, 27.i.1958, 1 spec. (B. M. May).
Te Kuiti: Waipuna Cave, 200yds, 2.xi.1957, 1 spec. (V. A. L. May); near entrance, 11.i.1958, 1 spec. (B. M. May).

Deleatidium (Atalophlebioides) cromwelli Phill.? Tx-int.

Matira: Gaskell's Stalactite Cave, 300yds, 30.xi.1958, 1 spec. (S. A. Rumsey).
Te Kuiti: Waipuna Cave, near entrance, 11.i.1958, 1 spec. (B. M. May); Luckie Strike Cave, 550yds, 14.ii.1959, 1 spec. (K. A. J. Wise); Hollow Hill Cave, 150yds, 3.xi.1957, 2 specs. (B. M. May); 300yds, 15.ii.1959, 1 spec. (K. A. J. Wise).

Nymphs of most of the above species have been recovered from cave streams. Development was completed within the cave but the imagines apparently died without breeding.

ODONATA

CORDULIIDAE

Hemicordulia australasiae Ramb. Tx-int.

Waitanguru: Briar's Cave, 150yds, 1.i.1961, 2 specs. (B. M. May).

PLECOPTERA (det. K. A. J. Wise)

GRIPOPTERYGIDAE

Nesoperla spiniger Till. Tx-int.

Te Kuiti: Waipuna Cave, 200yds, 2.xi.1957, 1 pupa (V. A. L. May).

Zelandobius confusus (Hare) Tx-int.

Te Kuiti: Hollow Hill Cave, 25yds, 12.i.1958, 1 spec. (R. W. Taylor).

EUSTHENIIDAE

Stenoperla prasina Newm. Tx-int.

Te Kuiti: Hollow Hill Cave, 100yds, 12.i.1958, 1 spec. (K. A. J. Wise); Gardner's Gut Cave, 300yds, 25.x.1959, 1 spec. (D. Smith); Waipuna Cave, on wall, 8.xii.1957, exuviae (F. E. Walton); 11.i.1958, exuviae (K. A. J. Wise).

ORTHOPTERA

RHAPHIDOPHORIDAE (det. A. M. Richards)

Gymnoplectron acanthocera (Milligan) Tph.

Port Waikato: Small cave, near entrance, 1.viii.1959, 1♂, 1♀ (B. M. May).

Gymnoplectron waitomoensis (Richards) Tph.

Port Waikato: Small cave, near entrance, 1.viii.1959, 1♂ (B. M. May).
Matira: Gaskell's Glow-worm Cave, 20yds, 6.vii.1958, 2♂♂, 2♀♀ (B. M. May).
Kawhia: Rubay's Cave, 20yds, 27.i.1958, 1♂ (B. M. May).
Te Kuiti: Aranui Cave, near entrance, 2.xi.1954, 3♂♂, 2♀♀ (A. M. Richards); 30.iii.1957, 2♂♂, 1♀ (A. M. Richards); Ruakuri Cave, near entrance, 2.xi.1954, numerous immature specs. (A. M. Richards).

Pallidoplectron turneri Richards Tph.

Te Kuiti: Waitomo Cave, 3.xi.1954, 1♂, 1♀ (A. M. Richards); Waitomo Cave, glow-worm grotto, 30.iii.1957, 1♂ (A. M. Richards); Luckie Strike Cave, near entrance, 14.ii.1959, 2♂♂, 2♀♀, *in copulo* (B. M. May).

Waitanguru: Briar's Cave, 200yds, 1.i.1961, 2♂♂, 2♀♀, *in copulo* (B. M. May).

The biology and morphology of the cave wetas have been exhaustively studied (Richards 1958, 1961). Their distribution as shown by cave collecting, is of interest; Port Waikato, where the two species occur in the same cave, is the southern limit of *G. acanthocera* and the northern limit of *G. waitomoensis*. *G. acanthocera* is the common species in the Waitakere Ranges, Auckland.

DICTYOPTERA

BLATTIDAE

Cutilia sedilloti Bol. Tx-t.

Port Waikato: Port Waikato Cave, 300yds, 9.iii.1958, 1 spec. (P. Skinner).

HEMIPTERA

MESOVELIIDAE

Microvelia macgregori Kirk Tx-int.

Port Waikato: Puriri Cave, 100yds, 9.iii.1958, 1 spec. (B. M. May).

NEUROPTERA (det. K. A. J. Wise)

CORYDALIDAE

Archichauliodes diversus (Walk.) Tx-int.

Te Kuiti: Luckie Strike Cave, 100yds, 60ft above stream, 2.xi.1957, 1 larva (B. M. May); 200yds, 14.ii.1959, 1 spec. (K. A. J. Wise); Hollow Hill Cave, 20yds, 15.ii.1959, 2 specs. (B. M. May).

LEPIDOPTERA (det. K. A. J. Wise)

LYONETIIDAE

Opogona omoscopa Meyr. Tx-int.

Port Waikato: Puriri Cave, 100yds, 15.vi.1958, 2 spec. (S. A. Rumsey).

TRICHOPTERA (det. K. A. J. Wise)

PHILOPOTAMIDAE

Hydrobiosella stenocerca Till. Tph?

Te Kuiti: Waipuna Cave, near entrance, 1.vi.1956, 2 specs. (D. V. May); 50yds, 9.xii.1956, 1♂, 1♀ (B. M. May); 100yds, 23.ii.1957, 1♂ (B. M. May); 200yds, 18.v.1957, 2♂♂ (B. M. May); 200yds, 2.xi.1957, 1 spec. (V. A. L. May); near entrance, 11.i.1958, 6 specs. (B. M. May); 7 specs. (K. A. J. Wise); 3 specs. (R. W. Taylor); Luckie Strike Cave, 500yds, 2.xi. 1957, 5 specs. (B. M. May); 450yds, 14.ii.1959, 2 specs. (B. M. May); 500yds, 14.ii,1959, 3 specs. (K. A. J. Wise); Waipapa Road Cave, 200yds, 19.iv.1958, 1 spec. (B. M. May); Hollow Hill Cave, 500yds, 15.ii.1959, 1 spec. (K. A. J. Wise).

RHYACOPHILIDAE

Hydrobiosis sp. Tx-int.

Te Kuiti: Luckie Strike Cave, 500yds, 2.xi.1957, 1 spec. (B. M. May); White's Cave, 300yds, 18.iii.1961, 1 spec. (S. Folkenhaugh).

Hydrobiosis gallanis Mosely Tx-int.

Port Waikato: Puriri Cave, 50yds, 31.vii.1960, 1 spec. (B. M. May).

Hydrobiosis parumbripennis McFarl. Tx-int.

Te Kuiti: Hollow Hill Cave, 50yds, 12.i.1958, 1 spec. (K. A. J. Wise); 20yds, 15.ii.1959, 3 specs. (K. A. J. Wise).

Hydrobiosis soror Mosely Tx-int.

Te Kuiti: Hollow Hill Cave, 300yds, 12.i.1958, 1 spec. (B. M. May); 50yds, 12.i.1958, 1 spec. (K. A. J. Wise).

HYDROPSYCHIDAE

Hydropsyche sp. Tx-int.

Te Kuiti: Hollow Hill Cave, 50yds, 12.i.1958, 1 ♀ (K. A. J. Wise); Fred Cave, 170ft down, 250yds, dead on wall, 26.iii.1960, 1 ♂, 1 ♀ (B. M. May).

Hydropsyche colonica McL. Tx-int.

Te Kuiti: Hollow Hill Cave, 25yds, 12.i.1958, 2 specs. (R. W. Taylor).

Hydropsyche fimbriata McL. Tx-int.

Port Waikato: Puriri Cave, 50yds, 1.viii.1959, 1 spec. (B. M. May).
Te Kuiti: Lemberg's Cave, 27.vii.1957, 1 spec. (F. E. Walton); Waipuna Cave, near entrance, 11.i.1958, 1 ♂ (K. A. J. Wise); Luckie Strike Cave, 200yds, 14.ii.1959, 1 spec. (K. A. J. Wise).

POLYCENTROPODIDAE

Polyplectropus sp. Tx-int.

Te Kuiti: Hollow Hill Cave, 50yds, 3.xi.1957, 1 ♀ (B. M. May).

LEPTOCERIDAE

Triplectides sp. Tx-int.

Te Kuiti: Waipuna Cave, 100yds, 23.ii.1957, 1 spec. (B. M. May).

PSYCHOMYIDAE

Zelomyia trulla McFarl. Tx-int.

Matira: Gaskell's Stalactite Cave, 300yds, 30.xi.1958, 1 spec. (S. A. Rumsey).
Te Kuiti: Luckie Strike Cave, 450yds, 14.ii.1959, 1 spec. (B. M. May).

In company with other aquatic insects, trichopteran larvae often penetrate caves for a short distance in the stream before pupating. The resulting imagines do not, as a rule, tolerate conditions sufficiently to breed. They were frequently seen resting on walls and stalactites where they remained to die.

Hydrobiosella stenocerca is probably an exception. Adults and larvae were found consistently as far as 500 yards from an entrance. The larvae are predacicus and therefore independent of plant life. The species is nocturnal, hence a basis for a troglophilic community would appear to be present.

DIPTERA

TIPULIDAE (det. C. P. Alexander)

Dolichopeza (Dolichopeza) atropos (Hudson) Tx-t

Te Kuiti: Hollow Hill Cave, 50yds, 3.xi.1957, 1 spec. (S. A. Rumsey).

Gynoplistia (Gynoplistia) concava Alex. Tx-t.

Te Kuiti: Hollow Hill Cave, 50yds, 3.xi.1957, 1 spec. (S. A. Rumsey).

Gynoplistia (Gynoplistia) tridactyla Edw. Tx-t.

Te Kuiti: Hollow Hill Cave, 300yds, 15.ii.1959, 1 spec. (K. A. J. Wise).
Piopio: Davis's System, 100yds, 4.vi.1961, 1 spec. (L. G. Watson).

Limnophila effeta Alex. Tx-t.

Port Waikato: Port Waikato Cave, 500yds, 9.iii.1958, 1 spec. (B. M. May).

Limnophila tonnoiri Alex. Tx-t

Te Kuiti: Waipuna Cave, near entrance, 11.i.1958, 1 spec. (R. W. Taylor); Hollow Hill Cave, 400yds, 12.i.1958, 1 spec. (B. M. May).

Limonia (Dicranomyia) nigrescens (Hutton) Tx-t

Te Kuiti: Luckie Strike Cave, 75yds, 19.v.1957, 1 spec. (D. Lambert).

Longurio (Austrotipula) hudsoni (Hutton) Tx-t

Te Kuiti: Bridal Cave, near entrance, 9.xii.1956, 2 specs. (B. M. May).

Mischoderus annuliferus (Hutton) Tx-t

Kawhia: Owhiro, small cave, 50yd, 24.i.1958, 1 spec. (B. M. May).
Te Kuiti: Hollow Hill Cave, 50yds, 25.x.1959, 1 spec. (D. Smith).

Molophilus (Molophilus) tenuistylus Alex. Tx-t.

Kawhia: Rubay's Cave, 500yds, 27.i.1958, 1 spec. (B. M. May).
Te Kuiti: Hollow Hill Cave, 50yds, 3.xi.1957, 1 spec. (S. A. Rumsey).

Rhabdomastix (Sacandaga) brunneipennis Alex. Tx-t.

Te Kuiti: Hollow Hill Cave, 300yds, 12.i.1958, 1 spec. (K. A. J. Wise).

PSYCHODIDAE

Psychoda zonata Sat. Tph.

Te Kuiti: Virginia Cave, 110ft below entrance, 19.iv.1959, 2 specs. (B. M. May); Cut-throat Cave, 70ft below entrance, 25.viii.1962, 2 specs. (B. M. May).

Psychoda sp. Tph.

Te Anga: Taumatatotara, Arch Cavern, 50–200yds, on opossum droppings, 1.x.1961, larvae and pupae (B. M. May); 21.x.1961, 2 imagines, larvae and pupae (B. M. May).

MYCETOPHILIDAE (det. R. A. Harrison)

Arachnocampa luminosa (Skuse) Tph.

Abundant in all localities.

A comprehensive study of the life history of this fly, the celebrated glow-worm of the tourist caves, has been made by Gatenby (1959) and Richards (1960).

Exechia hiemalis Marshall Tx-t.

Te Kuiti: Cut-throat Cave, 25.viii.1962, 1 ♂ (B. M. May).

SCIARIDAE

Sciara sp. Tph.

Pirongia: Karamu Cave, 350yds, 21.iv.1957, 2 specs. (B. M. May); ex trap, 350yds, 21.iv.1957, 1 spec. (B. M. May).
Te Kuiti: Waipuna Cave, on debris, 400yds, 18.v.1957, 6 imagines, larvae (B. M. May); ex trap, 500yd, 6.vii.1957, 1 spec. (P. Skinner); on debris, 200yds, 11.i.1958, 4 imagines, larvae (B. M. May); Whites Cave, 200yds, 18.iii.1961, 1 spec. (D. Gardiner); upper level, on rat droppings, 200yds, 24.iv.1962, 2 larvae (B. M. May).
Port Waikato: Puriri Cave, 400yds, 9.iii.1958, 1 spec. (B. M. May).
Te Anga: Taumatatotara Arch Cavern, on opossum droppings, 50–200yds, 1.x.1961, larvae and pupae (B. M. May); 21.x.1961, 3 imagines, larvae and pupae (B. M. May).

Sciara sp. is very different in habit from the mycetophilid *Arachnocampa*. The larva is similarly surrounded by a protective film of mucus, but it is not predacious. It lives among organic debris of all kinds where it is thought to feed on moulds.

SIMULIIDAE (larvae det. J. M. Kelsey)

Austrosimulium australense (Schmer.) Tx-int.

Te Kuiti: Hollow Hill Cave, 200yds, 12.i.1958, 1 spec. (B. M. May); 250yds, ex stream, 12.i.1958, larvae (K. A. J. Wise); 15.ii.1959, larvae (K. A. J. Wise).
Matira: Gaskells Cow Cave, 300yds, 9.viii.1958, 2 specs. (B. M. May).
Port Waikato: Puriri Cave, 150yds, 1.viii,1959, 1 spec. (B. M. May).

CHIRONOMIDAE

Anatopynia debilis (Hutton) det. R. A. Harrison Tph.

Te Kuiti: Hollow Hill Cave, 200yds, 12.i.1958, 1 spec. (B. M. May).

Anatopynia apicinella Freeman Tph.

Te Kuiti: Hollow Hill, 12.i.1958, 1 ♂ (B. M. May).

Harrisius pallidus Freeman, det.. P. Freeman Tph.

Te Kuiti: Hollow Hill Cave, 300yds, 12.i.1958, 1 spec. (B. M. May); 600yds, 1 spec. (B. M. May).
Te Anga: Taumatatotara Cave, 600yds, 30.ix.1961, 1 spec. (D. Kellie); 400yds, 1.x.1961, 1 spec. (D. Gardiner).
Waitanguru: Briar's Cave, 4.ii.1961, 1 spec. (B. M. May).

Paucispinigera approximata Freeman Tph.

Te Kuiti: Hollow Hill, 400yds, 3.vi.1962, 1 ♂, 1 ♀ (B. M. May); Honikiwi, 500yds, 7.x.1962, 1 ♀ (B. M. May).
Te Anga: Taumatatotara Cave, 1.x.1961, 1 ♀ (D. Gardiner).

Tanytarsus sp., det. R. A. Harrison. Tph.

Port Waikato: Puriri Cave, 150yds, 15.vi.1958, 1 spec. (B. M. May).
Te Kuiti: Luckie Strike Cave, 500yds, 14.ii.1959, 1 spec. (K. A. J. Wise); White's Cave, 7.iv.1962, 1 ♂ (B. M. May).

Chironomids, together with some of the smaller tipulids and the sciarids, are the main food sources of the glow-worm *A. luminosa*.

PHORIDAE

Megaselia rufipes (Mieg.) Tx-t.

Pirongia: Karamu Cave, 300yds, ex trap, 20.iv.1957, 3 specs. (B. M. May).
Te Kuiti: Cut-throat Cave, 100yds, ex trap and on cattle bones, 6.x.1962, 6 specs. (B. M. May).

SPHAEROCERIDAE (det. R. A. Harrison)

Leptocera thomasi Harrison Tx-t.

Port Waikato: Puriri Cave, ex trap, 350yds, 15.vi.1958, 1 imagine, larvae (B. M. May).

CALLIPHORIDAE (det. R. A. Harrison)

Calliphora quadrimaculata Swed. Tx-int.

Pirongia: Karamu Cave, 200yds, 21.iv.1957, 2 imagines (P. Weston).

This species is numerous wherever carcases of farm stock have recently decomposed. Although individuals may penetrate for considerable distances, they do not survive long after their source of food has disappeared.

SIPHONAPTERA

DOLICHOPSYLLIDAE

Nosopsyllus fasciatus (Bosc.) Tx-int.

Pirongia: Karamu Cave, 400yds, 10.xi.1961, 1 spec. (B. M. May).

A single dead specimen of the rat flea was found in a dry wall alcove. Rats are frequent visitors to most caves, although they are very seldom seen. The species is probably *Rattus rattus* L. (Wodzicki 1950). The finding of bones, thought to be those of *R. exulans* Peale (Maori *Kiore*) indicates that this species also may have been present.

COLEOPTERA

CARABIDAE: SCARITINAE (det. C. J. Watt)

Clivina rugithorax Putz. Tx-int.

Port Waikato: Puriri Cave, 350yds, 15.vi.1958, 1 spec. (B. M. May).

CARABIDAE: LICININAE

Dichrochile cordicolle Broun Tx-t.

Matira: Gaskell's Stalactite Cave, ex trap, 700yds, 30.xi.1958, 1 spec. (B. M. May).

Dichrochile cephalotes Broun, det. E. B. Britton Tx-t.

Waitanguru: Briar's Cave, 50yds, 17.iv.1960, 1 spec. (B. M. May).

CARABIDAE: TRECHINAE (det. E. B. Britton)

Duvaliomimus mayae Britton Tb.

Te Kuiti: Waipuna Cave, ex trap, 500yds, 23.ii.1957, 1 Paratype ♀ (B. M. May); 28.ix.1957, 1 Paratype ♂, 1 Paratype ♀ (F. E. Walton); 2.xi.1957, Holotype ♀, 3 Paratypes ♀ (V. A. L. May); Luckie Strike Cave, on damp mud, 150yds, 2.xi.1957, 1 ♀ (P. Weston); ex trap, 150yds, 6.iv.1958, 5 Paratypes ♂, 4 Paratypes ♀ (D. V. May); ex trap, 500yds, 13 Paratypes ♂, 26 Paratypes ♀ (D. V. May); 150yds, 14.ii.1959, 1 ♀ (B. M. May); Hollow Hill Cave, 300yds, 15.ii.1959, remains of 2 specs. (B. M. May); Whites

Cave, 150yds, 30.viii,1959, 1 spec. (D. L. Smith); ex trap, 200yds, 24.iv.1962, 2 ♀ (B. M. May); Warren's Cave, ex trap, 150yds, 1 spec. (L. Mander); Gardner's Gut Cave, on damp mud, 150yds, 10.x.1959, 1 spec. (B. M. May); 600 yds, 25.ii.1960, 1 ♂ (P. J. Barrett); 600yds, 10.iii.1962, 1 ♀ (D. V. May); 600yds, 2.vi.1962, 1 ♂ (D. V. May); Rumbling Gut Cave, on damp mud, 100yds, 28.xi.1959, 1 spec. (B. M. May); Blind Man's Bluff Cave, damp mud, 23.iii.1962, 1 ♂ (J. Hobson); Urenui Cave, 900yds, 7.iv.1962, 1 spec. (J. Pybus).

Duvaliomimus styx Britton Tph.

Port Waikato: Puriri Cave, on mud beside stream, 200–300yds, 15.vi.1958, Holotype ♂, 4 Paratypes ♀ (B. M. May); on wet flowstone, 100yds, 1.viii.1959, 1 ♂ (B. M. May); on mud, 200yds, 31.vii.1960, 2 ♂ ♂ (B. M. May).

Duvaliomimus n.sp. Tb.

Piopio: Paemako, small cave, 50yds, 9.vii.1961, 1 spec (K. A. J. Wise); 30yds, in trap, 18.xi.1962, 1 ♀ (M. McCallum); Sid's Surmise Cave, 150–200yds, on wall, 18.xi.1962, 2 ♀ ♀ (D. Gardiner); on mud by stream, 1 ♂, 1 ♀ (B. M. May).

Duvaliomimus n.sp. Tb.

Te Kuiti: Fred Cave, on damp mud, 300yds, 26.iii.1960, 1 ♂ (B. M. May).

Neanops caecus (Britton) Tb.

Te Kuiti: Fred Cave, 400yds, 170ft below surface, 17.ii.1960, Holotype ♀ (D. V. May, P. J. Barrett); 300yds, 26.iii.1960, Paratype ♀ (B. M. May).

Bembidiinae

Eotachys crypticolus Britton Tph.

Port Waikato: Puriri Cave, on mud near stream, 15.vi.1958, Holotype ♀ (S. A. Rumsey); 150yds, 1.viii.1959, 1 Paratype ♀ (B. M. May).

Harpalinae

Nemaglossa atriceps McLeay Tx-t.

Port Waikato: Port Waikato Cave, 300yds, 9.iii.1958, 1 spec. (B. M. May).

Syllectus anomalus Bates, det. C. J. Watt Tx-t.

Port Waikato: Puriri Cave, ex trap, 350yds, 1 spec. (B. M. May).
Matira: Gaskell's Stalactite Cave, ex trap, 700yds, 30.xi.1958, 1 spec. (B. M. May).

Agoninae: Sphodrini (det. E. B. Britton)

Prosphodrus waltoni Britton Tph.

Te Kuiti: Lemberg's Cave, 100yds, 27.vii.1957, 1 Paratype ♀ (F. E. Walton); Waipuna Cave, 500yds, 11.i.1958, Holotype ♂ (B. M. May); Green Rift Pot, depth 100ft, 70yds, 2.iv.1961, 1 spec (J. Hobson).
Piopio: Davis's System, 900yds, 4.vi.1961, 2 specs. (L. G. Watson).

Pterostichinae

Plocamostethus planiusculus White, det. C. J. Watt Tx-t.

Pirongia: Karamu Cave, 21.x.1956, 1 spec. (D. Barford).

Rhytisternus miser Chaud., det. C. J. Watt Tx-t.

Pirongia: Tomac Tomo, depth 70ft, below entrance, 20.iv.1957, 1 ♂ (B. M. May).
Piopio: Paemako, King George Cavern, 50yds, 1 ♂ (B. M. May); 1 ♂ (D. Gardiner).

Staphylinidae

Leptacinus socius Fauv. Tx-t.

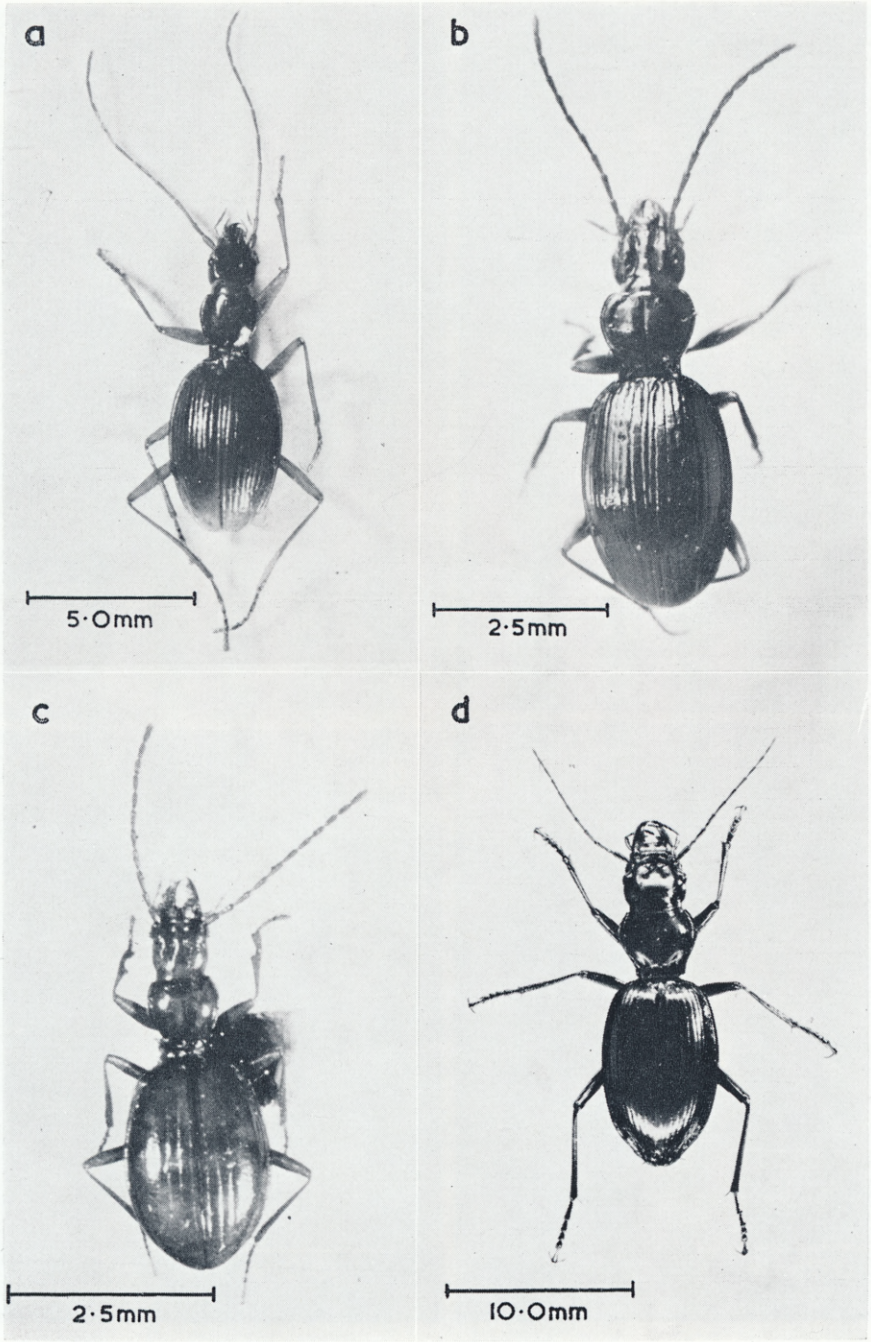
Port Waikato: Puriri Cave, ex trap, 15.vi.1958, 1 spec. (B. M. May).

Paraconosoma polita Steel, det. W. O. Steel Tx-t.

Te Kuiti: Waipuna Cave, with collembola on rat droppings, 100yds, 11.i.1958, 1 spec. (B. M. May).

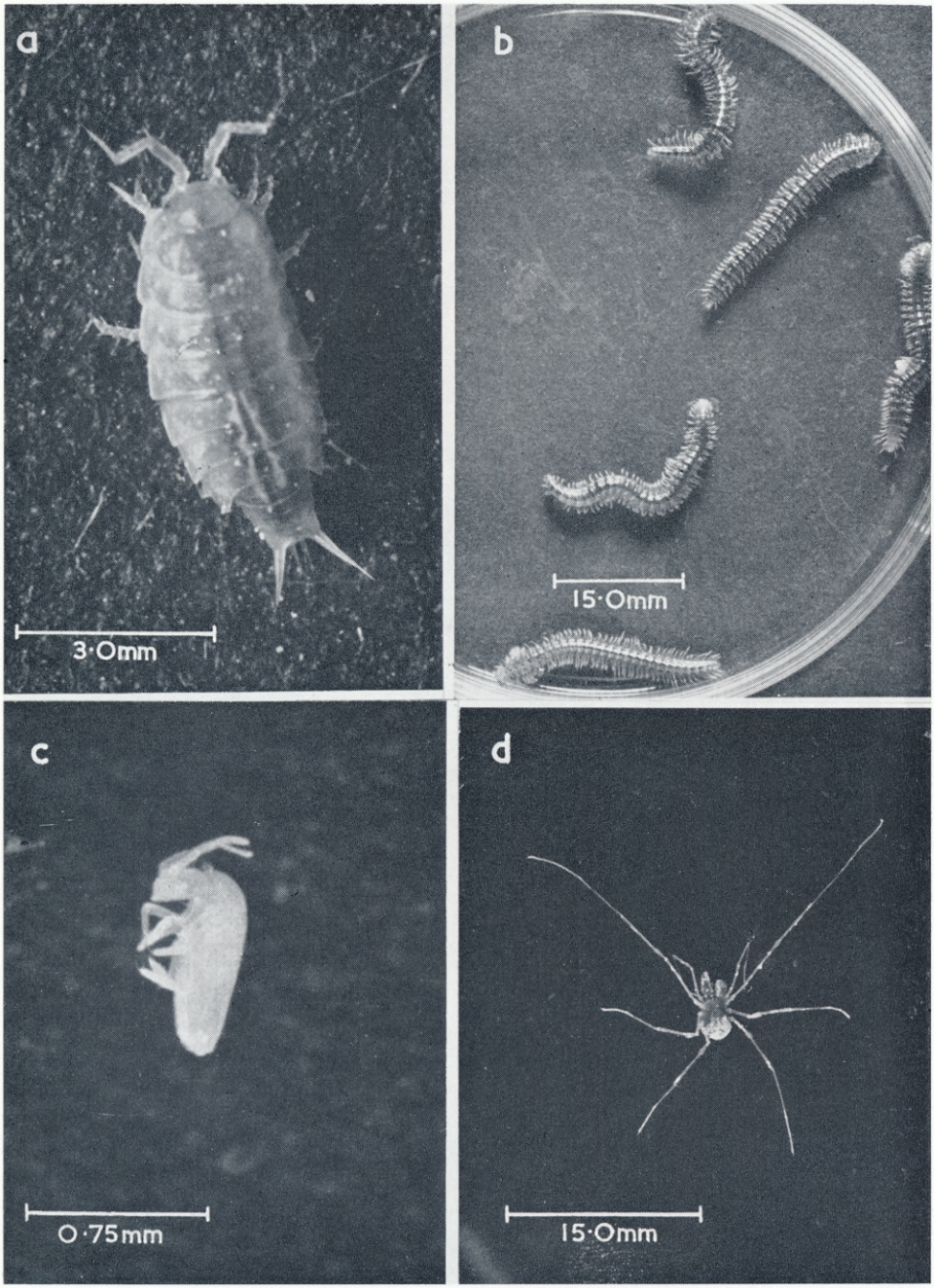
Atheta sp. Tph.

Te Anga: Taumatatotara, Arch Cavern, on opossum droppings, 100yds, 21.x.1961, 7 specs., larvae (B. M. May).



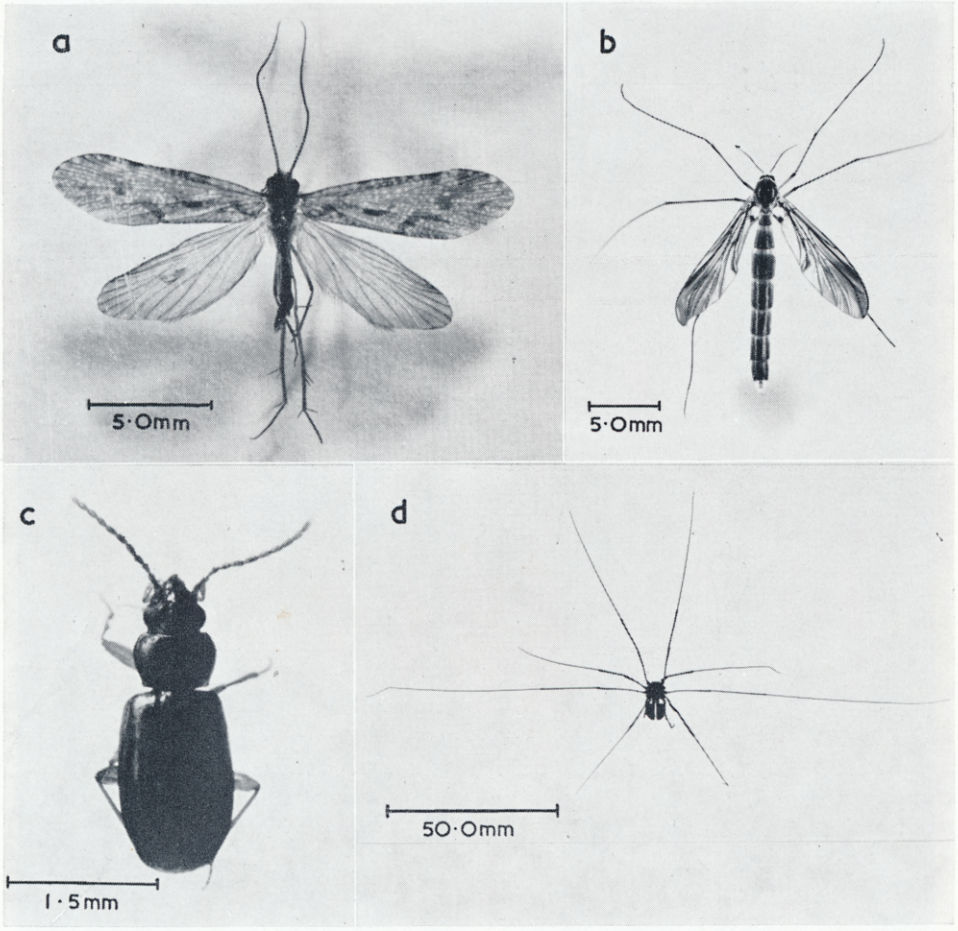
Photos by S. A. Rumsey.

Coleoptera. a—*Duvaliomimus mayae* Britton. b—*D. styx* Britton. c—*Neanops caecus* Britton. d—*Prosphodrus waltoni* Britton.



Photos a, b, c by J. W. Endt; d, by S. A. Rumsey.

a—Isopoda, *Styloniscus phormianus* (Chilton). b—Diplopoda, *Schedotrigona* sp. c—Collembola, *Spelaphorura petallata* Salmon. d—Opiliones, *Hendea myersi cavernicola* Forster.



Photos by S. A. Rumsey.

a'—Trichoptera, *Hydrobiosella stenocerca* Till. b—Diptera, *Arachnocampa luminosa* Skuse. ♀ c—Coleoptera, *Eotachys crypticolus* Britton. d—Opiliones, *Megalopsalis* sp.

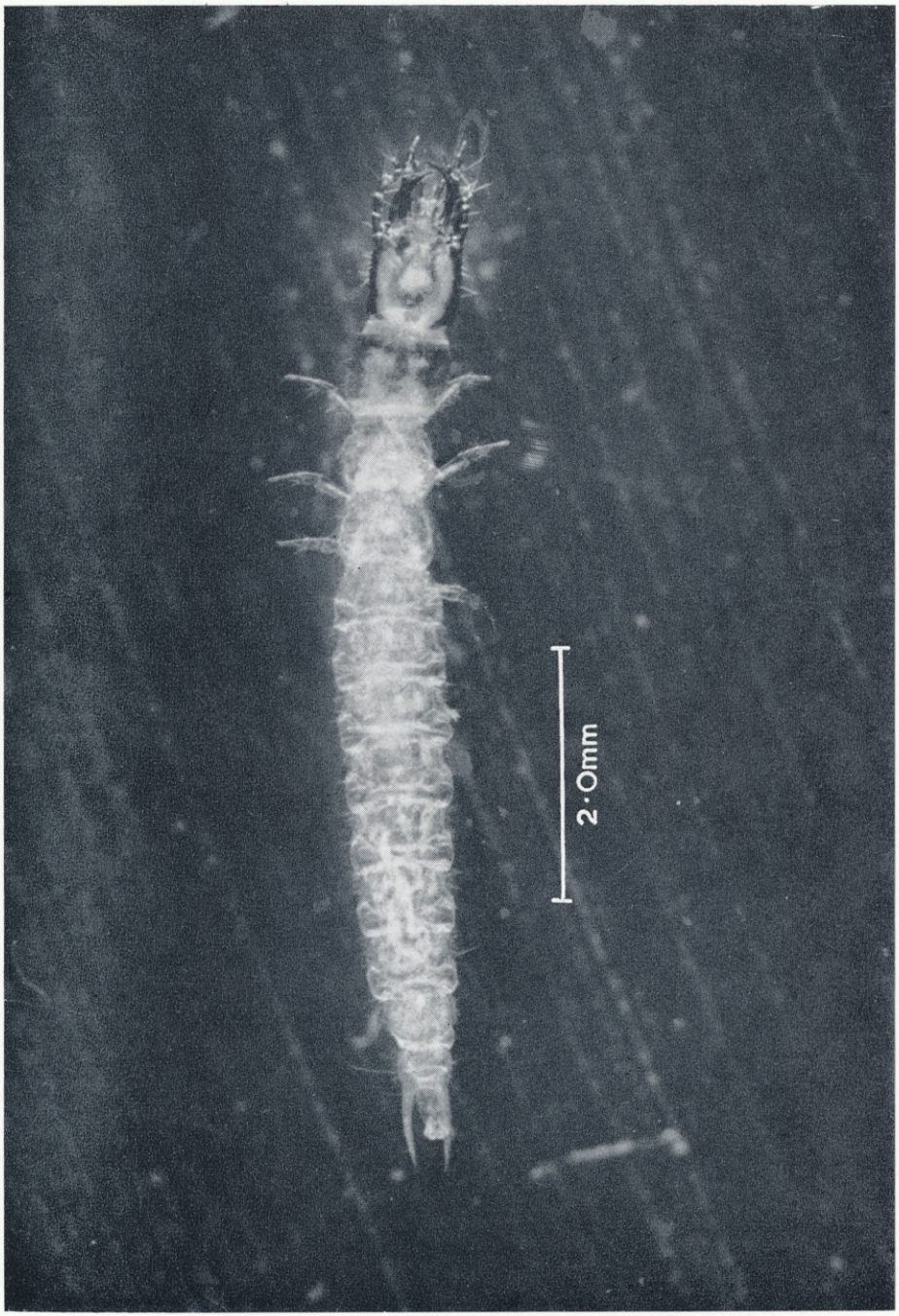


Photo by J. W. Endt.

Duvaliomimus mayae Britton, larva.

HISTERIDAE

Epierus purus Broun Tx-int.

Port Waikato: Puriri Cave, ex trap, 350yds, 15.vi.1958, 1 spec. (B. M. May).

CORYLOPHIDAE

Corylophodes lawsoni Broun Tx-int.

Port Waikato: Puriri Cave, ex trap, 350yds, 15.vi.1958, 1 spec. (B. M. May).

SILPHIDAE

Necrophilus prolongatus Sharp, det. C. J. Watt Tph.

Te Kuiti: Waipuna Cave, ex trap, 500yds, 6.vii.1957, 1 spec. (P. Skinner); 8.xii.1957, 4 specs. (F. E. Walton); Hollow Hill Cave, 300yds, 15.ii.1959, 1 spec. (B. M. May); Fred Cave, depth 170ft, near entrance, 26.iii.1960, 4 specs. (V. McGregor).

Piopio: King George Cavern, 17.xi.1962, 1 spec. (D. Gardiner).

CATOPIDAE (det. R. D. Pope)

Mesocolon puncticeps Broun Tph.

Port Waikato: Puriri Cave, on mud beside stream, 150yds, 15.vi.1958, 1 spec. (B. M. May); ex trap, 350yds, 1 spec. (B. M. May); on rat dropping 100yds, 1.viii.1959, 2 specs. (B. M. May).

DASCILLIDAE (det. R. D. Pope)

Byrrhocryptus urquharti Broun Tx-int.

Te Kuiti: Luckie Strike Cave, 450yds, on wall, 14.ii.1959, 1 spec. (B. M. May).

ELATERIDAE

Lacon van de Polli Cand. Tx-int.

Port Waikato: Puriri Cave, 250yds, 9.iii.1958, 1 spec. (P. Skinner).

Te Kuiti: Virginia Cave, below entrance, depth 110ft, 19.iv.1959, 8 specs. (B. M. May).

DYTISCIDAE (det. C. J. Watt)

Rhantus pulverosus Steph. Tx-int.

Te Kuiti: Ernie's Waterfall Cave, in pool, 500yds, 22.iv.1957, 1 spec. (B. Hainsworth).

EROTYLIDAE

Tritomidia rubripes Reitt. Tx-int.

Matira: Gaskell's Glow-worm Cave, 200yds, 6.vii.1958, 2 specs. (B. M. May).

SCARABAEIDAE: APHODIINAE (det. A. M. Richards)

Saprosites rugosus Richards Tx-int.

Port Waikato: Puriri Cave, near trap, 150yds, 15.vi.1958, 1 spec. (D. V. May); ex trap, 350yds, 15.vi.1958, 1 spec. (B. M. May).

ARACHNIDA–ARANEIDA (det. R. R. Forster)

PISAURIDAE

Dolomedes minor Koch Tph.

Te Kuiti: Luckie Strike Cave, 50yds, 2.xi.1957, 1 spec. (S. A. Rumsey).

Dolomedes sp. Tph.

Port Waikato: Onewhero, Keal's Cave, 28.vii.1957, 1 imm. ♂ (B. M. May).

Pirongia: Karamu Cave, 100yds, 17.viii.1957, 1 imm. ♀ (D. V. May).

THERIDIIDAE

Theridion sp. Tph.

Te Kuiti: Lost World Cave, depth 180ft, 2.vi.1957, 1 imm. ♀ (P. Skinner); Hollow Hill Cave, 200yds, 3.xi.1957, 1 ♀ and egg sac (B. M. May).

LINYPHIIDAE

Paralinyphia sp. Tph.

Port Waikato: Puriri Cave, 450yds, 15.ix.1957, 1 spec. (P. Skinner).

MIMETIDAE

Mimetus sp. Tph.

Matira: Gaskell's Glow-worm Cave, 100yds, 6.vii.1958, 1 spec. (B. M. May).
Te Kuiti: Lost World Cave, 2.vi.1957, 1 spec. (H. G. Lambert).

AGALENIDAE

Cambridgea foliata (Koch) Tph.

Pirongia: Karamu Cave, 19.iv.1957, 1 ♂ (P. Skinner).

Cambridgea sp. Tph.

Port Waikato: Puriri Cave, 450yds, 15.ix.1957, 1 imm. spec. (P. Skinner).

CLUBIONIDAE

Uliodon frenatus (Koch) Tph.

Pirongia: Karamu Cave, 19.iv.1957, 1 ♂ (P. Skinner).

DIPLURIDAE

Hexathele hochstetteri Aus., det. R. L. Pilgrim Tph.

Pirongia: Karamu Cave, 21.x.1956, 1 spec. (D. Barford).
Te Kuiti: Lost World Cave, 13.iii.1954, 1 spec. (H. G. Lambert).

TOXOPIDAE

Cycloctenus flaviceps (Koch) Tph.

Pirongia: Karamu Cave, 150yds, 17.viii.1957, 1 ♀ (P. Skinner).

A large proportion of spiders are, by nature, facultative cavernicoles. All those recorded from caves are known also to be bush dwelling species.

ACARINA (det. Commonwealth Institute of Entomology, Brit. Mus.)

LAELAPTIDAE

Hypoaspis (Androlaelaps) sp. Tph.

Pirongia: Tomac Tomo, on rat droppings with Collembola, 100yds, 20.iv.1957 (B. M. May).

Laelaptid mites are usually parasitic on both vertebrates and invertebrates (Baker and Wharton, 1952).

VEIGAIAIDAE

Veigaia planicola (Berlese) Tph.

Pirongia: Karamu Cave, ex trap, 700yds, 17.viii.1957 (B. M. May).

Willmann (1936) reports mites of this genus from numerous caves in Europe, but little is known of their biology.

DIGAMASELLIDAE

Digamasellus sp. Tx-?t.

Te Kuiti: Waipuna Cave, ex trap, 550yds, 2.xi.1957, nymphs (B. M. May).

"Live in damp soil or moss where they probably prey on other small arthropods or their eggs" (Baker and Wharton *loc. cit.*).

SCUTACARIDAE

Scutacarus sp. Tx-?t.

Te Kuiti: Waipuna Cave, ex trap, 550yds, 2.xi.1957 (B. M. May).

"Minute, bizarre creatures found in moss, soil and sod samples throughout the world, and on various insects" (Baker and Wharton *loc. cit.*).

ANOETIDAE

Histiostoma sp. Tx-?t.

Te Kuiti: Waipuna Cave, ex trap, 550yds, 2.xi.1957 (B. M. May); ex trap, 500yds, 8.xii.1957 (F. E. Walton); White's Cave, on rat droppings in upper level, 300yds, 7.iv.1962 (B. M. May); 24.iv.1962 (B. M. May).

Inhabits damp, decaying vegetation. The deutonymphs are travellers on insects (Baker and Wharton *loc. cit.*).

CYMBAEREMAEIDAE

? **Scapheremaeus** sp. Tx-?t.

Te Kuiti: Waipuna Cave, ex trap, 550yds, 2.xi.1957 (B. M. May).

The members of this genus are often fungus or lichen feeders (Baker and Wharton *loc. cit.*). In this instance the specimens were probably brought into the cave with flood water.

PYEMOTIDAE

Pygmephorus nr.**chaetosus** Krczal Tph.

Matira: Gaskell's Cave, on mouldy rat droppings, —.xii.1961 (B. M. May).

Te Kuiti: White's Cave, on mouldy rat droppings in upper level, 300yds, 7.iv.1962 (B. M. May); 24.iv.1962 (B. M. May).

The habits of *Pygmephorus* are not well known. It is said to migrate on small animals and insects and to be carnivorous (Baker and Wharton *loc. cit.*). The cave population, however, appeared to be associated with mould rather than with Collembola, also present on rat droppings.

OPILIONES (det. R. R. Forster)

TRIAENONYCHIDAE

Hendea myersi cavernicola Forster Tb.

Pirongia: Karamu Cave, 700yds, 21.iv.1957, 2 specs. (B. M. May); 50yds, 17.viii.1957, 1 spec. (P. Skinner).

Te Kuiti: Waipuna Cave, 500yds, 11.i.1958, 1 spec. (B. M. May); Hollow Hill Cave, 300yds, 15.ii.1959, 3 specs. (B. M. May); Whites Cave, 100–200yds, 10.iv.1962, 3 specs. (B. M. May).

This small species, which is pale red-brown and slow moving, is fairly numerous. It is unknown except from caves.

Hendea sp. Tph.

Matira: Gaskell's Glow-worm Cave, 150yds, 6.vii.1958, 1 imm. spec. (B. M. May).

Te Kuiti: Waipuna Cave, ex trap, 500yds, 6.vii.1957, 1 imm. spec. (P. Skinner).

PHALANGIIDAE

Megalopsalis sp. Tph.

Pirongia: Karamu Cave, near entrance, 19.iv.1957, 1 spec. (P. Skinner); 120yds, 17.viii.1957, 1 ♂ (D. V. May).

Te Kuiti: Waipuna Cave, ex trap, 500yds, 9.vii.1957, 4 imm. specs. (P. Skinner); Lemberg's Cave, 120yds 27.vii.1957, 1 spec (F. E. Walton); Hollow Hill Cave, 100yds, 3.xi.1957, 2 specs. (S. A. Rumsey); 200yds, 12.i.1958, 1 spec. (B. M. May); 300yds, 12.i.1958, 1 spec. (K. A. J. Wise); 300yds, 12.i.1958, 2 specs. (R. W. Taylor); Lost World Cave, depth 200ft, 6.vii.1958, 1 spec. (J. Pybus).

MOLLUSCA (det. R. A. Cumber and K. A. J. Wise)

ANCYLIDAE

Gundlachia neozealandica Suter Tph.

Te Kuiti: Hollow Hill Cave, in stream, 12.i.1958, numerous specs. (K. A. J. Wise).

HYDROBIIDAE

Potamopyrgus antipodum (Gray) Tph.

Port Waikato: Puriri Cave, in stream, 1.viii.1959, numerous specs. (B. M. May).

Te Kuiti: Hollow Hill Cave, in stream, 12.i.1958, numerous specs. (K. A. J. Wise); Virginia Cave, in stream, 19.iv.1959, numerous specs. (B. M. May).

Pirongia: Karamu Cave, in clay on wall, 600yds, 11.xi.1961, 2 subfossilised specs. (D. Gardiner, B. M. May).

Potamopyrgus spelaeus spelaeus (Frauenfeld) Tph.

Pirongia: Karamu Cave, in clay on wall, 600yds, 11.xi.1961, 2 subfossilised specs. (D. Gardiner, B. M. May).

Discussion

General Considerations

It will be seen from the following table (Table I) that while trogloxenes or "casual visitors" form approximately half (51.2%) and troglophiles 43.2%, the troglobites or obligate cavernicoles represent only a small part (6.4%) of the total cave fauna of the Port Waikato–Piopio limestone area. If the Te Kuiti–Piopio area alone were considered, the proportion of troglobites would be somewhat higher, due to the presence of carabid beetles, which have not occurred north of the Waitomo district.

Table I.—Summary of Fauna from Limestone Caves in the Area Between Port Waikato and Piopio.

	Trogloxenes (Intolerant)	Trogloxenes (Tolerant)	Troglophiles	Troglobites	No. of Species
Onychophora		1			1
Total Onychophora					1
Isopoda			1		1
Amphipoda			2		2
Decapoda			1		1
Total Crustacea					4
Chilopoda		1			1
Diplopoda	1		5		6
Symphyla			1		1
Total Myriapoda					8
Collembola			7	3	10
Ephemeroptera	6				6
Odonata	1				1
Plecoptera	3				3
Orthoptera			3		3
Dictyoptera		1			1
Hemiptera	1				1
Neuroptera	1				1
Lepidoptera	1				1
Trichoptera	10		1		11
Diptera	2	13	9		24
Siphonaptera	1				1
Coleoptera	8	8	6	4	26
Total Insecta					89
Araneida			10		10
Acarina		4	3		7
Opiliones			2	1	3
Total Arachnida					20
Mollusca			3		3
Total Mollusca					3
Total in each category	35	28	54	8	
Total number of species					125
Percentage in each category	28.5%	22.7%	43.2%	6.4%	

Comparison With Italian Cave Fauna

The fauna of Italian caves (Baggini, 1961) yields some interesting comparisons. Troglophiles are the predominant category (48%), with trogloxenes 36%. Troglobites (16%) are still the smallest group, but nevertheless represent more than twice the New Zealand percentage. The actual number of species for Italy is far greater, 726 against 123, but only a small part of New Zealand is under consideration. The difference is partly due to the prevalence in Italy of certain individual groups such as Copepoda, Annelida, Collembola and Acari.

The relatively small number of terrestrial forms recorded in New Zealand is undoubtedly due to the virtual absence of bats from our caves, and hence a smaller, less varied food supply. In countries where bats colonise caves in large numbers, their guano maintains a permanent community of coprophages and their predators. Although bat skeletons are often discovered, they are nearly always solitary and there is no evidence that large colonies ever existed. The only significant source of animal droppings is the rat. Fresh and decayed droppings are indeed the basis of a food cycle. Collembola, Isopoda, Myriapoda and Acarina all feed on these, and are in turn devoured by beetles and their larvae.

Evolution

Regressive evolution is exhibited in many of the cave species. This, in some cases, may be more apparent than real. Beatty (1948) showed that lack of colouration in subterranean aquatic amphipods is due to their ancestral pigment being of the carotenoid type which is light sensitive. Viré (1904) found that pigmentation of some cave species occurred after exposure to light (cited Beatty, *loc. cit.*). Maguire (1961) however, considered from his experiments, that carotene was not light-sensitive and that pigmentation was dependent on nutrition. Carotenoids in an available form must therefore be lacking for hypogean populations, even though present in cave sediments. The Puriri Cave amphipod community of colourless specimens would appear to offer a parallel situation.

In terrestrial isopods that contain a melanin type of pigment (Baldwin and Beatty, 1941; Maguire *loc. cit.*), and in Coleoptera (Krekeler 1958; Barr 1960b), it is postulated that the loss of pigment and degeneration of eyes, both characters of neutral survival value in total darkness, may be caused by genetic factors, through the action of mutation pressure unopposed by selection pressure. It is further stated by Allee *et al* (1949): "If selection favours an increased development of one character while another character has a diminished survival value in a given habitat, there will be a shift in the alleles in many gene systems with a consequent degeneration of the character that is losing importance." This is particularly evident in trechine beetles such as *D. mayae,* where legs, mandibles, antennae and tactile hairs are greatly increased in length. The New Zealand cavernicolous isopod *Styloniscus phormianus* displays varying degrees of depigmentation and ocular reduction (to 2 ocelli). Vandel (1958a) has stated that ocelli do not diminish in number until depigmentation of the cuticle is complete.

With regard to lack of wings, Lindroth (1949), mentioned by Southwood (1962) concluded that stability and isolation of habitat favoured flightlessness, and that the gene for the fully winged state would be selected against in such environments.

Subterranean living has produced not only morphological changes but contraction of the life cycle also. This phenomenon is associated in the Trechinae, with a reduction in the number of ovarioles (Deleurance, 1958). In extremely adapted Coleoptera, a single large egg, rich in nutriment, is laid. The resulting larva neither feeds nor moults but encloses itself in a cell in which it eventually

pupates and from which it emerges as an adult. Furthermore, the digestive tract, well developed in the embryo, becomes atrophied in the larval stage (Deleurance 1961).

A remarkable degree of parallelism is displayed between the evolution of New Zealand troglobic carabids and that of some forms in the northern hemisphere. A programme of breeding would be necessary to determine the extent to which larval development is also parallel.

It should be mentioned here that although most of the obligatory and many of the facultative cavernicoles exhibit varying degrees of modification, it does not follow that all stages of regression can be attributed to isolation in the cave environment (Leleup 1956; Jeannel 1959). In the constant high humidity and low temperatures of biotopes such as rain forest litter or overhung stream beds, the slow rate of metabolism might equally well disrupt the gene balance, and hence adaptation of the trechines *Duvaliomimus* and *Neanops* may have begun in the epigean domain. The New Zealand weevil genera *Idus* and *Hectaeus* are anophthalmous, apterous and weakly pigmented, and the pselaphids *Pselaphus delicatus* Broun and *P. caecus* Broun exhibit features which are regarded by Park (1960) as cavernicolous, yet all are inhabitants of the forest floor. They are the edaphobites (Greek: edaphos, floor; bios, life) or "*fossiles vivants du sol*" of Coiffait (1955; 1958).

It is widely accepted (Hesse *et al* 1937; Jeannel 1949; Barr 1960a) that permanent colonization of caves by Coleoptera must have occurred during the Pleistocene period. But whereas Hesse suggested that they were killed by glaciation except where they survived in caves, later workers consider that carabid beetles flourished on the cool fringes of ice sheets or glaciers and only retreated into caves or to high altitudes during the hot, dry interglacial periods. Present day cave populations are therefore most likely to be found where major limestone beds are adjacent to areas of ancient glaciation.

In the South Island of New Zealand such areas occur most obviously where limestone borders the Southern Alps on the West Coast and also in Nelson Province, where the limestones of Paturau and Takaka Hill districts are close to the N.W. Nelson mountains, which are considered by Willett (1950) to have undergone minor glaciation and a lowering of the snowline to 3,700ft. Willett further maintained that tundra conditions must have prevailed over the greater part of the South Island with forest persisting only on the coastal area of N.W. Nelson and in places where glaciation was confined to the mountain valleys. It therefore appears likely that pre-Pleistocene Coleoptera would have been exterminated in most other areas by severe conditions and by flooding, even if caves were colonized initially. An increasing number of troglobic beetles and other arthropods are, in fact, being discovered in the caves of Paturau and Takaka Hill by members of the New Zealand Speleological Society, encouraged by the example and enthusiasm of Mr Ian Townsend of Entomology Division, D.S.I.R., Nelson.

In the North Island, Willett (*loc. cit.*) placed the Pleistocene snowline at 4,300ft (2,900ft lower than at present), with only the Tararuas, Mt Egmont and Central Plateau being actively glaciated (Fig. 1). The forest would have been driven radially outwards from these centres, but would have flourished elsewhere. Several limestone areas are within 50 to 100 miles of the ancient Pleistocene snowline. There are excavated limestones in the high country behind Wairoa in northern Hawkes Bay; at the head waters of the Manawatu River near Ormondville and Dannevirke, and also in the Te Kuiti formation south of Kawhia Harbour. Of these, only the Te Kuiti limestone has been systematically explored both for caves and fauna.

Trechine beetles of the genus *Duvaliomimus* are not all restricted to caves. *D. watti* Britton inhabits deep bush streambeds in the Hunua Range near Auckland, and two bush species, *D. brittoni* Jeannel and *D. walkeri* (Broun) are found in the South Island. *D. styx* from Puriri Cave, Port Waikato, may be a very recent cavernicole. A catastrophic climatic change took place for these shade-loving beetles, when bush was cleared for farming about 100 years ago. Individuals living in the vicinity of the cave, which doubtless they were already in the habit of visiting, would have sought permanent shelter there, becoming virtually isolated by the unwelcome glare and dryness beyond the entrance. The species has normal eyes and does not yet show signs of regression. *D. mayae* is the most numerous troglobic species inhabiting the Te Kuiti–Piopio caves. It has undergone considerable modification but still possesses eyes, though these are greatly reduced. *Neanops caecus*, known only from Fred Cave, is completely anophthalmous and weakly pigmented, but its appendages are not elongated to the same extent as in *D. mayae*. It has the facies of an edaphobite.

Jeannel's (1959) remarks on the cave fauna of New Zealand would appear to be somewhat premature considering the paucity of collection and of published work in the past. Present indications are that the Coleoptera, particularly of South Island Caves, are not only fairly numerous, but are proving to be of interest phyletically. The number of forms is likely to be limited by the relatively small extent of cave areas, compared with those of Europe and N. America, rather than by climatic considerations.

Chronology

The Te Kuiti limestone was laid down in the Oligocene (Waitakian) (Finlay and Marwick 1940) 25 to 40 million years ago, finally emerging from the sea during the Miocene (Fleming 1949). Cave excavation would have begun perhaps 13 million years ago, in the Pliocene or even earlier (upper Miocene). The evolution of some cave forms could have started then, the insect fauna being closely similar to that of Recent times (Tillyard 1926). Beetles preferring a cool, moist habitat are more likely to have resorted to caves during the first interglacial stage of the lower Pleistocene, nearly 2 million years ago.

Affinities

"The similarities between the cave faunae of widely separated regions are attributed to the fact that only members of certain groups are able to adapt themselves to cave conditions, and that such adaptation produces parallel structure and appearance." (Hesse *et al loc. cit.*).

Peripatoides is a trogloxene in New Zealand, but a troglobic Onychophoran genus, the only one known, is described from South Africa. This is *Peripatopsis alba* Lawrence 1931, which is depigmented, anophthalmous and bears relatively long, slender legs.

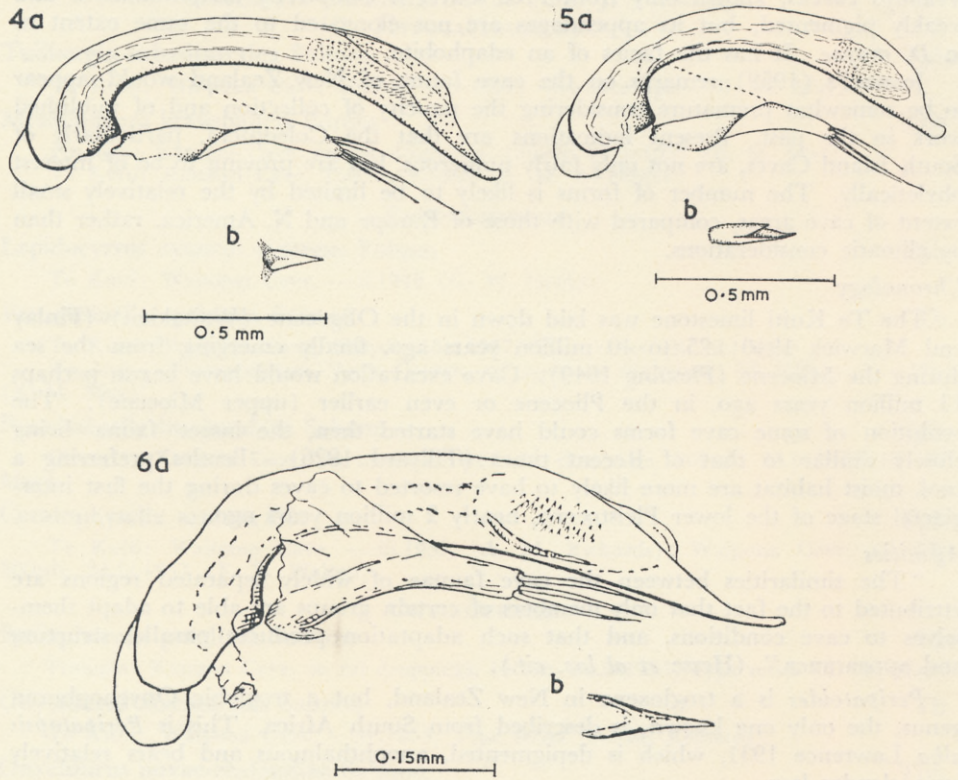
Isopoda (terrestrial). The genus *Styloniscus* Dana is extremely close to *Cordioniscus* Graeve of which a troglobic species is recorded from Greece (Vandel 1958b).

Amphipoda (aquatic). A group which in Europe and N. America is well represented by numerous species in the family Gammaridae, is as yet represented in New Zealand caves by two genera only, in the same family.

Collembola. Of the ten species collected, three are new to science (Salmon 1958) and may be regarded as troglobic. The extent to which they are in fact obligatory cavernicoles can only be determined by further study, such as evaluation of cave dependent characteristics as indicated by Christiansen (1961). All the genera occurring here are also recorded from American or European caves (Strinati 1953; Deboutteville 1952; Cullingford 1953; Christiansen 1960).

Trichoptera. Of numerous species found in Italian caves, many are considered to be troglophiles and *Wormaldia subterranea* Rad. is listed by Baggini (*loc. cit.*) as a troglobite. This species is in the same family (Philopotamidae) as the New Zealand *Hydrobiosella stenocerca.*

Coleoptera. The genus *Prosphodrus* was erected by Britton (1959) to contain *P. waltoni,* the first recorded sphodrine indigenous to the southern hemisphere. A second species, *P. occultus* Britton discovered in caves in Hawkes Bay, was added to the genus a year later (Britton 1960). *Prosphodrus* is fairly closely related to *Ceuthosphodrus* Jeann. of which numerous cavernicolous species are known from the Iberian peninsula, in localities ranging from southern Spain to the French Basses-Pyrénées. The most northern species are considerably modified (Mateu 1953).



Figs. 4–6.—Aedeagi of *Duvaliomimus* and allied genera. 4a—*Duvaliomimus mayae* Britton, aedeagus. b—Copulatory piece. 5a—*Duvaliomimus styx* Britton. aedeagus. b—Copulatory piece. 6a—*Apoduvalius negrei* Jeannel, aedeagus. b—Copulatory piece (after Jeannel).

Eotachys crypticolus from Puriri Cave, Port Waikato, with its large, fully developed wings, and its very close affinities with Mediterranean and Asiatic species (Britton 1960) is somewhat enigmatic. In March, 1962, however, a series of this beetle was taken at light in Te Atatu, Auckland; a circumstance which suggests that *E. crypticolus* may perhaps be a recent immigrant and that although its behaviour in the cave was harmonious, its presence there was accidental.

Syllectus anomalus is recorded here as a trogloxene, but the recent discovery, in South Island caves, of a related troglobic species, *Pholeodytes townsendi* Britton, 1962, may indicate a greater extension of the cavernicolous habit.

The genera *Duvaliomimus* and *Neanops* are closely related to the phyletic group of *Duvalius* Jeannel. Larvae of *D. mayae* differ from those of *Duvalius spiessi* Jeannel from the Carpathian Mts of Roumania only in conformation of nasale and retinaculum (May, 1963). *Neanops* is strikingly similar to *Apoduvalius* Jeannel 1953 from caves in the Cantabrian Mts. on the northern seaboard of Spain. In *Neanops*, the labial tooth is still further effaced and the apical portion of stria 1 is obsolete although the recurved carina still terminates below stria 5. The only significant difference appears to be the absence in *Neanops* of pubescence on the inner side of the apices of anterior tibiae. Although both *Duvaliomimus* and *Neanops* show some morphological similarity to *Pseudanophthalmus* Jeannel, from the Appalachian Mts in N. America, they belong to a different phyletic complex. A recent Japanese discovery, *Thalassoduvalius* Uéno is apparently so near *Duvaliomimus* that decisive characters to separate them are difficult to find (Uéno 1956). Differences mentioned by Uéno no longer apply when *D. mayae* is compared.

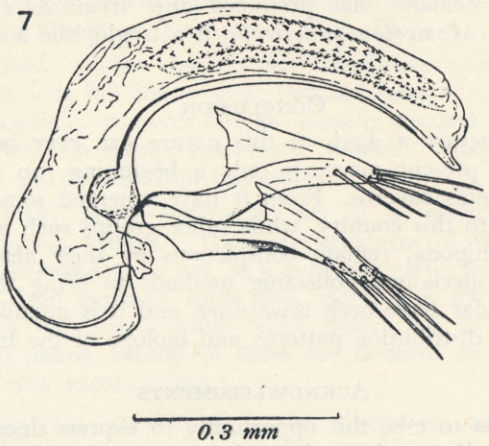


FIG. 7.—*Thallasoduvalius masidae* Uéno, aedeagus (after Uéno).

Male genitalia offer useful characters for comparison. Unfortunately only female specimens of *Neanops caecus* have been taken, but aedeagi of *D. mayae* and *D. styx* are described as follows: *Duvaliomimus mayae* Britton (Fig. 4). Aedaegus slender, moderately arcuate with apex considerably produced; basal bulb obtusely flexed; internal sac armed with short teeth which become bristle-like towards apex; copulatory piece (Fig. 4b) represented by a triangular, acuminate, chitinised portion of the sac wall; parameres slender with 3 long apical and either 1 or 2 shorter, subapical setae.

Duvaliomimus styx Britton (Fig. 5). Aedeagus shorter than, but similarly shaped to that of *D. mayae*, apical lamella less produced, more *retroussé*; basal bulb obtusely flexed; internal sac shorter than *D. mayae*, similarly armed; transfer apparatus (Fig. 5b) distinct from wall of sac consisting of two elongate, triangular copulatory pieces, of unequal length, joined at base, with apices acute; parameres slender, with 3 long apical and 1 subapical setae.

Species of *Duvalius* possess transfer apparatus of a similar type to that of *Duvaliomimus styx*, whereas that of *D. mayae* is closer to *Apoduvalius* (Fig. 6b). *Thalassoduvalius* (Fig. 7) differs in having no specialised copulatory piece, but the number of parameral setae is variable as in *D. mayae*.

Jeannel (1949) has postulated an Oligocene north Atlantic land bridge to explain the obvious relationship between N. American and European elements of the Trechini, and a similar route in the north Pacific (1953b) to account for the Japanese element as exhibited in *Kurasawatrechus* Yoshida et Nomura. Indeed, the presence of such a bridge has been reaffirmed recently by Haag (1962) who showed that at least a narrow, intermittent stretch of land must have existed in the region of Bering Strait. Any such attempt to link the New Zealand element with that of the northern hemisphere would involve too much unwarranted guessing at the present time. The New Zealand cave trechines would appear to be a remnant survival of a once widely distributed population, the parent stock of which could, perhaps, have originated in Europe, but on existing evidence, could equally well have had its origin in Asia. On the other hand, populations may have migrated northward and southward independently, under climatic pressure, from a source nearer the equator.

In direct contrast to the European and North American faunas, there is no evidence that New Zealand has produced any troglobic catopids. The only cavernicolous species, *Mesocolon puncticeps*, is a troglophile and is not in any way modified.

Conclusion

It is doubtful whether a work of this nature can ever be regarded as complete. Certainly the present survey is only a beginning; an introduction to the fauna of New Zealand's caverns. From it have emerged some groups which are little known or new to this country, while other groups such as Copepoda and to a large extent Amphipoda, remain conspicuous by their absence but requiring, perhaps, only more specialised collecting methods to bring them to light. The Coleoptera in particular have been rewarding, and it is intended to make a more detailed study of the distribution patterns and biology of the troglobic forms.

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