An overview of flat bug genera (Hemiptera, Aradidae) from New Zealand, with considerations on faunal diversification and affinities[1]

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Abstract: Nineteen genera and thirty-nine species of Aradidae have been described from New Zealand, most of which are endemic (12 genera, 38 species). An overview of all genera and an identification key to subfamilies, tribes, and genera are presented for the first time. Species included in each genus are listed for New Zealand. Concise generic descriptions, illustrations emphasizing key diagnostic features, colour photographs representing each genus, an overview of the most relevant literature, and notes on distribution are also given. The biology and diversification of New Zealand aradids, and their affinities with neighbouring faunas are briefly discussed.

Key words: Aradidae, biogeography, Hemiptera, New Zealand, taxonomy.

Introduction

The Aradidae, also commonly referred to as flat bugs or bark bugs, form a large family of Heteroptera containing over 1,800 species and 210 genera worldwide (SCHUH & SLATER 1995). They are classified within the Pentatomomorpha and are seen by most authors as the sister group of Termitaphididae, but unlike other pentatomomorphans, Aradidae lack trichobothria (seta-bearing spots on the abdominal venter).

Most aradid species range from 3-11 mm, are flattened dorsoventrally, and share the following diagnostic features: two-segmented tarsi (except in some taxa); four-segmented antennae; ocelli absent; elongate feeding stylets (modified mandibles and maxillae) that are coiled within the clypeus when withdrawn – a characteristic shared with Termitaphididae – and usually broadly exposed connexivum around the edge of relatively small-sized hemelytra (when present).

Aradids are highly cryptic animals living either under the bark of decaying trees, or on twigs or wood debris on the floor of wet forests, and using their stylets to extract liquids from fungal hyphae associated with decaying wood. Many ground-dwelling species of rainforest environments are wingless – a condition thought to have evolved several times in the phylogeographic history of the group (e.g., see MONTEITH 1969b, 1982, 1997) – and have become highly modified morphologically and very strangely shaped. It now seems amazing that before 1938 most micropterous and apterous aradids were thought to be only nymphs. It was MILLER (1938) who first realised the phenomenon of aptery in adult Aradidae, a discovery that opened a totally new dimension to aradid taxonomy and accelerated the descriptive effort in many groups.

New Zealand and Australia are the only land masses so far known to harbour all eight recognised aradid subfamilies which, as far as their higher classification is concerned, have remained more or less the same since the comprehensive world revision of USINGER & MATSUDA (1959). As for tribes, KORMILEV & FROESCHNER (1987) defined two tribes within each of the Chinamyersi-

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[1] The authors dedicate this paper to their friend and colleague Ernst Heiss. His encouragement toward their research, his special interest in New Zealand aradids, and his contribution to the taxonomy of the world fauna are highly inspirational.

inae (Chinamyersiini and Tretocorini) and Prosympiestinae (Llaimacorini, Prosympiestini); all except Llaimacorini have been recorded from New Zealand.

GROZEVA & KERZHNER (1992), in revising VÁSÁRHELYI's (1987) phylogenetic scheme, provided the most recent hypothesis of phylogenetic relationships between aradid subfamilies (Fig. 44); their classification is followed here.

The New Zealand aradid fauna has recently been catalogued by LARIVIÈRE & LAROCHELLE (2004), who provided a detailed treatment of the nomenclature, geographic distribution, biology, and dispersal power of all described genera and species — the majority of which (12 out of 19 genera, 38 out of 39 species) are endemic to New Zealand.

The first indigenous taxon to be described from New Zealand was *Ctenoneurus hochstetteri* (MAYR 1866), followed by the descriptions of half a dozen or so genera and species by WHITE (1876), MYERS & CHINA (1928), USINGER (1943), and KORMILEV (1953). However, the taxonomy of New Zealand Aradidae only really took off with the world revision of USINGER & MATSUDA (1959), who described 10 new genera and 18 new species, and keyed all taxa known for the fauna at that stage. Subsequently, KORMILEV (1953, 1971), PENDERGRAST (1965a, 1965b, 1968), LEE & PENDERGRAST (1977), KIRMAN (1985a, 1985b, 1989a, 1989b), and HEISS (1990, 1998) published additional revisionary or descriptive papers bringing the total number of taxa to that currently known. No new taxon of New Zealand Aradidae has been described since 1998. Kormilev provided much of the descriptive work on a world basis following USINGER & MATSUDA (1959). MONTEITH (1966-1997) wrote the most useful contributions dealing with the diversification of aradid faunas in the Pacific Southwest and Australia.

Some have claimed that the New Zealand aradid fauna is amongst the best known in the world. The authors are of the opinion, however, after collecting Hemiptera in over 1,000 localities since 1992, and after inspecting this country's main entomological collections, that several taxa remain to be described and substantial amounts of unpublished information on distribution and biology remain locked in large holdings of unsorted material.

Taxonomic works on New Zealand aradids are scattered through the literature, the depth of taxonomic treatment is unequal between publications, and the format of taxonomic descriptions and the morphological terms used often lack uniformity as a result of which taxa cannot be easily compared within subfamilies, genera or even within the same publication. In addition, there is no identification key covering the subfamilies and genera known from New Zealand, keys to world subfamilies do not always work well with local taxa, and some keys to genera are fraught with problems (perhaps written with few specimens at hand).

Consequently, there is a need for a more uniform and encompassing approach to the taxonomy of New Zealand Aradidae. This paper aims to provide the first step towards such a goal, that is: a straightforward up-to-date overview of the New Zealand aradid genera; an identification key to supraspecific taxa; comparative subfamilial and generic descriptions; an overview of the most relevant literature; notes on geographic distribution, biology; and faunal affinities at the generic level.

Materials and Methods

Identification key and generic descriptions

The starting point for the identification key presented here was the "key to subfamilies" published by SCHUH & SLATER (1995), which in itself was an adaptation of USINGER & MATSUDA's (1959) key. All known New Zealand species were passed through SCHUH & SLATER's key and it soon became apparent that a number of taxa would not key out to the correct subfamily.

After testing the above subfamily key and modifying it to accommodate all known New Zealand genera, other keys to tribes and genera were tested for all species currently known within each subfamily. In addition to USINGER & MATSUDA (1959), the following papers containing keys were critically assessed: PENDERGRAST (1965a), Aneurinae; KORMILEV (1970) and KIRMAN (1989a), Carventinae; LEE & PENDERGRAST (1977) and MONTEITH (1997), Mezirinae; MONTEITH (1980), Chinamyersiinae; KIRMAN (1985b), Prosympiestinae.

The above process was supplemented by a careful analysis of published generic descriptions, together providing the basis for the character list utilised to write the keys and concise descriptions published here.

The morphological characters used in this study are thought to represent the most diagnostic and most easily observable morphological features at the generic level. A number of non-variable character states have been repeated between some genera to facilitate their separation from world genera or from potentially undescribed New Zealand genera. Except for the presence or absence of well-developed paratergites on the male pygophore (genital capsule), male genitalic characters have not been included at this early stage of the treatment of the New Zealand fauna because these are more taxonomically valuable at the species level.

Subfamily descriptions

Characters and character states were extracted from the 'manual' phylogeny of GROZEVA & KERZHNER (1992), which appeared to offer the best available source where a set of morphological attributes had been recorded consistently across all world subfamilies. The present authors are aware that other diagnostic characters can be used at the subfamily level, but they decided to include only GROZEVA & KERZHNER's (1992) characters in the basic subfamily descriptions presented here in order to test New Zealand genera against GROZEVA & KERZHNER's subfamily definitions. It soon became apparent that these subfamily definitions would need to be altered slightly to accommodate all currently known New Zealand genera.

GROZEVA & KERZHNER (1992) did not indicate which taxa were seen in their study. These authors may have worked mostly from the literature and it seems that not all world genera may have been considered – hence the New Zealand-based subfamily descriptions included in the present paper, which supplement and sometimes modify the world subfamily definitions derived from GROZEVA & KERZHNER's phylogeny.

The morphological characters that varied most from GROZEVA & KERZHNER's (1992) observations were: the length of the rostrum (Calisiinae, Mezirinae); the opening or closing of the rostral atrium (e.g., Carventinae, Mezirinae); the shape of the pulvillus (e.g., Chinayersiinae, Mezirinae); the dorsal and ventral patterns of glabrous areas (in several subfamilies).

Morphological terms

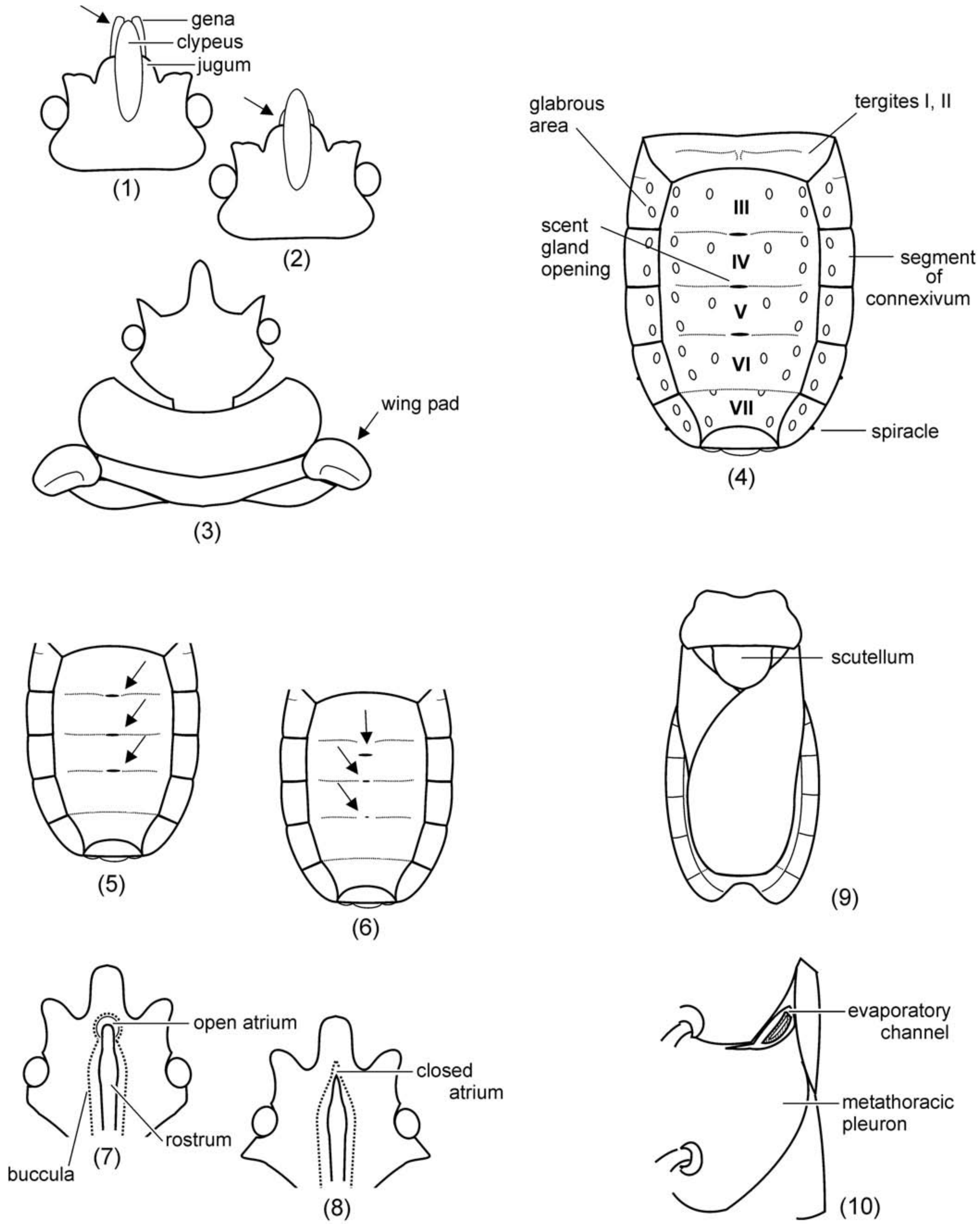
An attempt has been made to use the simplest terminology available from the most recent aradid literature and to use terms uniformly across all subfamilies. The main diagnostic features have been illustrated or may be seen on the colour photographs provided for each genus. A few morphological features deserving further explanations are discussed here:

Juga and genae. Adjacent to the clypeus dorsally are the juga (mandibular plates), and ventrally, the genae (maxillary plates) (Fig. 1), which may or may not be produced anteriorly to almost reach or exceed the apex of the clypeus. There has been some confusion in the literature about these structures, especially in identification keys, e.g., the term genae should have been used instead of mandibular plates (juga) in couplet 1 of SCHUH & SLATER's (1995) key to subfamilies.

Rostral atrium. When bordered by well-developed bucculae, the rostrum may arise from an atrium that is closed except for a slit-like opening (closed atrium, Fig. 8), or, it may arise from a wider chamber or depression (open atrium, Fig. 7).

Rostral groove. A longitudinal furrow running behind the rostrum along the underside of the basal part of the head (the gular or 'throat' area).

Scutellum. Usually well exposed between the hemelytra of macropterous (Fig. 9), submacropterous, and brachypterous species, while in micropters and apters the scutellum becomes almost completely fused with surrounding sclerites, being only recognisable as an elevation in the centre of the



Figs 1-10: Generalised drawings of main diagnostic characters: (**1, 2**) head, dorsal view; (**3**) head and thorax with hemelytra reduced to wing pads, dorsal view; (**4**) main features of abdomen, dorsal view; (**5, 6**) abdomen showing placement of scent gland openings, dorsal view; (**7, 8**) rostral atrium on underside of head; (**9**) thorax and abdomen of macropterous form with well-developed scutellum, dorsal view; (**10**) metathoracic pleuron with well-developed evaporatory channel, lateroventral view.

mesonotum. In many apterous New Zealand Carventinae, the backwardly produced medial region of the mesonotum may represent a highly modified form of the scutellum or scutellar region.

Mesonotum and metanotum. In apterous taxa (see photographs of many Carventinae) the original segmentation may be completely obscured by the sclerites becoming variously fused and highly modified with tubercles, ridges, depressions (pits) or grooves.

Wing development. Terminology follows LARIVIÈRE & LAROCHELLE (2004) for New Zealand Heteroptera. Macropters have both pairs of wings of approximately equal length, more or less reaching apex of abdomen. Submacropters have posterior wings visibly shorter than hemelytra, and hemelytra less developed than those of macropters but reaching more than 2/3 of abdomen length. Brachypters have hemelytra reaching 1/3-2/3 of abdomen length, the hemelytral membrane absent or reduced to a narrow edging, and the posterior wings substantially shorter than the hemelytra. Micropters display an extreme form of brachyptery where hemelytra are reduced (often to simple wing pads) and posterior wings are vestigial.

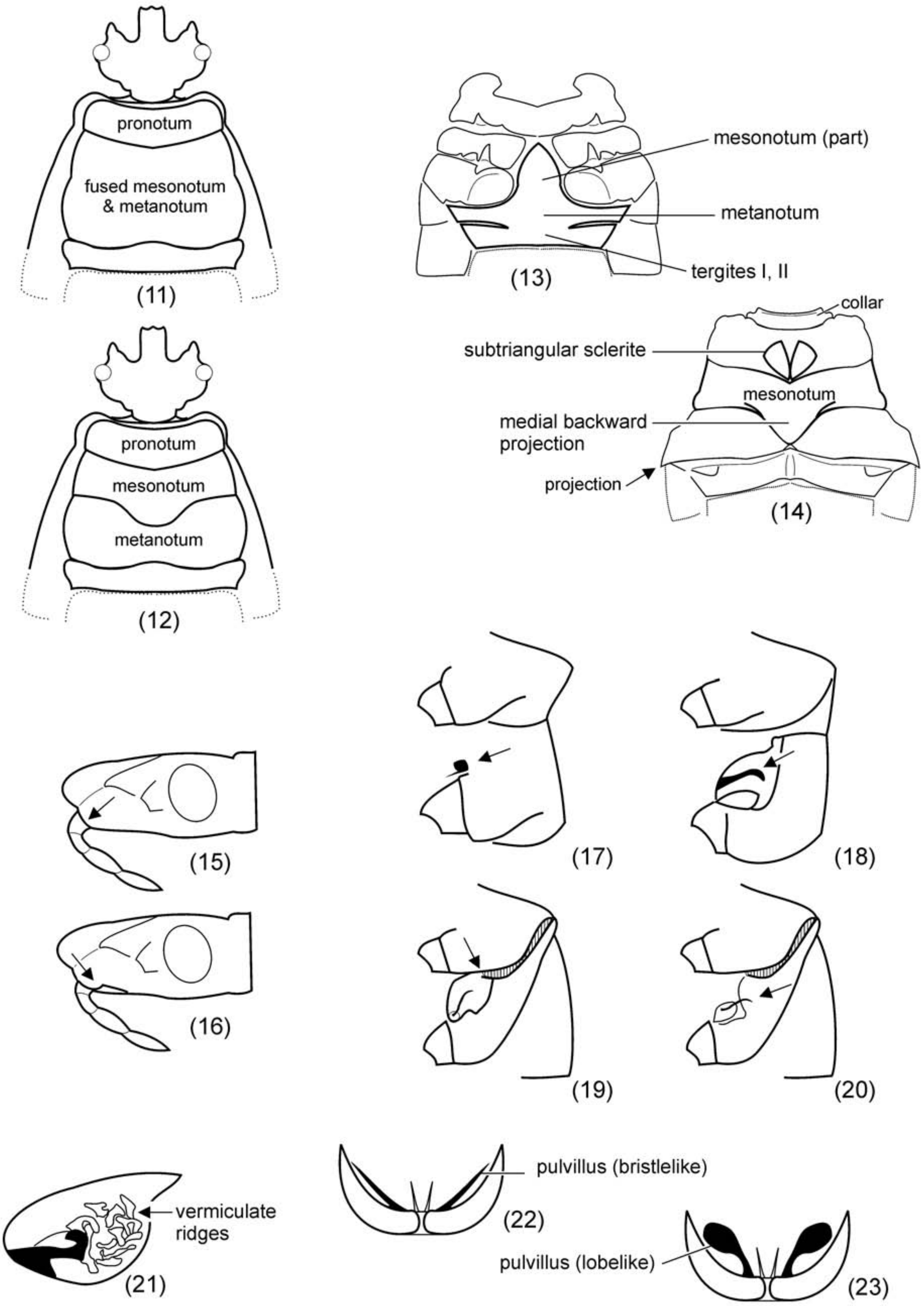
In aradids, the above definitions probably work better in terms of the relative development of each pair of wings rather than of their length in relation to that of the abdomen. Apters do not have wings or, in many aradids, wings are not visible; small rigid vestiges may have become fused with thoracic sclerites.

Parempodia and pulvilli. MONTEITH (1997) summarised the development of the nomenclature used to describe pretarsal structures. VÁSÁRHELYI (1986) applied a consistent terminology across all aradid subfamilies for the first time. The parempodia consist of a pair of bristles arising from the unguitractor plate between the bases of the claws. The pulvilli are larger, thicker, often spatulate structures attached beneath each claw (Figs 22-23). VÁSÁRHELYI (1986) recognised four states for this character: laminate, lobelike, bristlelike, and absence of pulvilli. GROZEVA & KERZHNER (1992) included two states in their phylogenetic analysis: lobelike and laminate, with the later state considered to be apomorphic. These authors neither included the absence of pulvilli nor the presence of bristlelike pulvilli in their analysis, but commented in their discussion that the lack of pulvilli in Aradinae is an apomorphic feature. Four character states are considered in the present study: spatulate pulvilli not laminate apically (=lobelike of above authors), spatulate pulvilli laminate apically (=laminate of above authors), bristlelike pulvilli, and pulvilli absent. The term spatulate, also used by MONTEITH (1997), is preferred over lobelike because it better defines a structure that is typically rounded or broad at the apex and tapered or attenuate at the base.

Dorsal abdominal scent gland openings. These openings (Figs 4-6) are functional and more evident in nymphs, but persist to various degrees in adults. Three more or less developed and equidistant paired openings are located along the posterior margin of abdominal tergites III-V; in some groups, e.g., Mezirinae and Carventinae, the first pair of openings are larger and strongly displaced posteriorly.

Tergal disc of abdomen. The abdominal segments III-VI (Fig. 4, excluding connexivum) are more or less fused, distinct from previous and subsequent segments, and forming a continuous plate called tergal disc.

Patterns of glabrous areas. Smooth patches can be found on abdominal segments (dorsally (Fig. 4) and ventrally), which have been termed glabrous areas by USINGER & MATSUDA (1959) and shown by ŠTYS (1974) to serve as points of muscular attachment to the cuticle. There can be various arrangements of these glabrous areas. In Mezirinae, for example, the dorsal pattern can be described by the formula 2:2:1, indicating there are two glabrous areas on the connexivum, two midlateral glabrous areas (next to the connexival suture), and one inner glabrous area on each side of the midline of abdominal segments III-VI. These glabrous areas are more visible in the nymph than in the adult, and in the latter they are usually more obvious dorsally than ventrally.



Figs 11-23: Generalised drawings of main diagnostic characters: (**11**, **12**) head and thorax of some Carventinae, dorsal view; (**13**, **14**) configuration of thoracic and first two abdominal sclerites of some Carventinae, dorsal view; (**15**) head with rostrum free at base, lateral view; (**16**) head with rostrum enclosed by bucculae at base, lateral view; (**17-20**) various configurations of metathoracic scent gland openings and associated evaporatory area, lateroventral view; (**21**) metathoracic scent gland opening with vermiculate ridges as in *Tretocoris*, lateroventral view; (**22**, **23**) pretarsal pulvilli, apical view of tarsal claws and associated structures.

Digital photographs

Colour photographs of one representative of each genus were captured through a Leica MZ-12.5 stereomicroscope, LeicaDC500 digital camera, and the increased-depth-of-field syncroscopy software Auto-Montage (Synoptics, U.K). Photos were further processed using CorelDRAW graphics suite version 11. As much as possible, specimens were cleared from body surface incrustations (Carventinae) and clinging debris (other subfamilies) before being photographed (see also Note(s) under Carventinae and Mezirinae).

Results

Identification key to subfamilies, tribes, and genera

Note. Morphological characters selected for identification are generally easy to observe, i.e. not requiring dissection before examination. When a subfamily or tribe contains a single genus in New Zealand, the generic name is immediately given; otherwise, the identifier is referred to a subsection of the main key, a subkey to genera within a subfamily. Additional supporting characters are given between square brackets.

1 Genae (below juga) produced anteriorly on either side of clypeus, nearly reaching or surpassing its apex (often forming a cleft or emarginate anterior margin of head (Fig. 1)) – genae can appear as extremely thin prolongations only clearly visible in laterodorsal view; dorsal abdominal scent gland openings (or scars thereof) three in number, not equally developed or spaced along posterior margin of tergites III, IV, V (first opening large, usually strongly displaced posteriorly; second rarely well developed; third obsolescent) (Fig. 6) 2

– Genae (below juga) not produced anteriorly on either side of clypeus, not nearly reaching or surpassing its apex (never forming a cleft or emarginate anterior margin of head) (Fig. 2); dorsal abdominal scent gland openings (or scars thereof) three in number, equally developed and equally spaced along posterior margin of tergites III, IV, V (Fig. 5) 12

2(1) Rostrum arising from an open atrium (Fig. 7; open area of bucculae); first dorsal abdominal scent gland opening (or scar thereof) not or only slightly displaced posteriorly. **Subfamily Aneurinae** 3

– Rostrum arising from a closed atrium (Fig. 8; nearly closed area of bucculae), through a longitudinal slit-like opening – if atrium opening is widened anteriorly then taxon is apterous or micropterous (*Acaraptera* and *Lissaptera* (Carventinae), *Woodwardiessa* (Mezirinae)); first dorsal abdominal scent gland opening (or scar thereof) displaced posteriorly to middle or hind margin of tergite IV (Fig. 6) 4

Subfamily Aneurinae

3(2) Scutellum poorly developed, appearing as a short, posteriorly arcuate elevation in the middle of the mesonotum (Fig. 32); hemelytra reduced to short lateral wing pads (Fig. 3) (tergal disc of abdomen completely exposed) (Fig. 32); connexivum delimited by deep longitudinal sutures dorsally and ventrally; ventrites IV, V, VI without a distinct transverse carina along anterior margin. [Habitus, Fig. 32; body length, about 5 mm] . . . . Genus *Aneuraptera*

– Scutellum well developed, subtriangular, broadly rounded apically (Fig. 9); hemelytra well developed, covering most of tergal disc (Fig. 9); connexivum delimited by deep sutures only dorsally; ventrites IV, V, VI with a distinct transverse carina along anterior margin. [Habitus, Fig. 33; body length, about 5 mm] . . . . Genus *Aneurus*

4(2) Metathoracic scent gland openings conspicuous, with well-developed, usually channel-like evaporatory area extending to lateral margin of metathoracic pleuron (Fig. 10). [Body surface sometimes obscured by clinging dirt but not or barely incrustate as in Carventinae.]. **Subfamily Mezirinae** 5

– Metathoracic scent gland openings inconspicuous, without well-developed channel-like evaporatory area. [Body surface with incrustation patterns more or less obscuring the integument.]. **Subfamily Carventinae** 6

Subfamily Mezirinae

5(4) Rostrum arising from an open atrium (Fig. 7); hemelytra reduced to short lateral wing pads (Fig. 42), not extending beyond posterior margin of abdominal tergite III (second visible); eyes stalked (Fig. 42). [Body hairy, especially around margin and on appendages; habitus, Fig. 42; body length, about 8-10 mm] . . . . Genus *Woodwardiessa*

– Rostrum arising from a closed atrium (Fig. 8); hemelytra with fully developed membranes (Fig. 41), extending posteriorly onto abdominal tergites VI-VII; eyes not stalked (Fig. 41). [Habitus, Fig. 41; body length, about 6-9 mm] . . . . Genus *Ctenoneurus*

Subfamily Carventinae

6(4) Rostrum arising from an open atrium (Fig. 7; open area of bucculae); fused connexival segments II + III extending forwards to posterior angles of pronotum (Figs 39-40) 7

– Rostrum arising from a closed atrium (Fig. 8; nearly closed, slit-like area of bucculae); fused connexival segments II + III not extending forwards to posterior angles of pronotum 8

7(6) Meso- and metanotum fused, forming a smooth, uninterrupted plate (Fig. 11). [Habitus, Fig. 40; body length, about 2.5-4.5 mm] . . . . Genus *Lissaptera*

– Meso- and metanotum distinctly separated, medial region of mesonotum produced backwards (Fig. 12). [Habitus, Fig. 39; body length, about 2.5-4.5 mm] . . . . Genus *Acaraptera*

8(6) Abdominal tergites I, II completely fused with metanotum and with mesonotum at middle, produced forwards as a subtriangular lobe (Fig. 13). [Habitus, Fig. 36; body length, about 3.7-4.8 mm] . . . . Genus *Leuraptera*

– Abdominal tergites I, II separated from metanotum by a distinct suture throughout, their medial regions not produced forwards 9

9(8) Meso- and metanotum fused at middle into a smooth hexagonal tumescence (Fig. 35), almost elliptical lobe in female, extending from anterior margin of mesonotum almost to posterior margin of metanotum; sutures between notal sclerites very deep. [Habitus, Fig. 35; body length, about 3.0-3.5 mm] . . . . Genus *Clavaptera*

– Meso- and metanotum not fused at middle into a smooth hexagonal tumescence as above; sutures between notal sclerites distinct but not very deep 10

10(9) Pronotum without posteriorly directed subtriangular sclerite behind collar; medial region of mesonotum produced backwards as a subtriangular lobe (Fig. 34) not extending as far as posterior margin of metanotum. [Habitus, Fig. 34; body length, about 4.0-5.0 mm] . . . . Genus *Carventaptera*

– Pronotum with posteriorly directed subtriangular sclerite behind collar (Fig. 14); medial region of mesonotum produced backwards as a subtriangular (Fig. 14) or subquadrate lobe extending to posterior margin of metanotum 11

11(10) Backward projection of medial region of mesonotum subtriangular (Figs 14, 38); tergal disc of abdomen with segments III-VI fused, without well delimited sclerites, or, partly unfused, with well delimited sublateral sclerites and with inner sclerites partly fused with median elevation; lateral margins of metanotum flaring posteriorly into more or less acutely rounded projections (more produced in males) (Fig. 14) [Habitus, Fig. 38; body length, about 2.5-3.5 mm] . . . . Genus *Neocarventus*

– Backward projection of medial region of mesonotum subquadrate to pentagonal (Fig. 37); tergal disc of abdomen with segments III-VI superficially unfused, with well delimited individual sublateral and inner sclerites; lateral margins of metanotum not flaring posteriorly into projections. [Habitus, Fig. 37; body length, about 2.5-3.5 mm] . . . . . . Genus *Modicarventus*

12(1) Rostrum entirely exposed at base (not bordered by well-developed bucculae) (Fig. 15); hemelytra with line of weakness at level of apex of scutellum (Fig. 31), often broken off at this level. [Habitus, Fig. 31; body length, about 4.5-6.5 mm] . . . . **Subfamily Isoderminae**, Genus *Isodermus*

– Rostrum not entirely exposed at base (bordered by well-developed bucculae) (Fig. 16); hemelytra, when present and well developed, without line of weakness at level of apex of scutellum 13

13(12) Metathoracic scent gland openings conspicuous with well-developed evaporatory area and channel (Figs 10, 18-20) 14

– Metathoracic scent gland openings inconspicuous, either small, forming a simple hole and without well-developed evaporatory area and channel (Fig. 17; Subfamily Aradinae), or scent gland opening indistinct (Subfamily Calisiinae) 18

14(13) Metathoracic scent gland openings with a long, curved seta in middle (Figs 19-20). **Subfamily Prosympiestinae** . 15

– Metathoracic scent gland openings with a raised ridge curved at apex (without a seta) (Fig. 18) **Subfamily Chinamyersiinae** 17

Subfamily Prosympiestinae

15(14) Antennae inserted on cylindrical tubercles (Fig. 30); metathoracic scent gland opening directly connecting to channel of evaporatory area (Fig. 19). [Habitus, Fig. 30; body length, about 3.0-4.5 mm] . . . . Genus *Neadenocoris*

– Antennae inserted on spine-like tubercles (Figs 28-29); metathoracic scent gland opening not directly connecting to channel of evaporatory area (Fig. 20) 16

16(15) Rostrum short, reaching or just reaching beyond posterior margin of head; lateral margins of pronotum straight or nearly so, anterolateral angles subacute, produced anteriorly (Fig. 29); third antennal segment distinctly shorter than other segments. [Habitus, Fig. 29; body length, about 5.5-8.0 mm] . . . . Genus *Mesadenocoris*

– Rostrum longer, reaching between front coxae; lateral margins of pronotum arcuate, more or less produced laterally at middle, anterolateral angles rounded, not produced anteriorly (Fig. 28); third antennal segment not distinctly shorter than other segments. [Habitus, Fig. 28; body length, about 4.7-6.5 mm] . . . . Genus *Adenocoris*

Subfamily Chinamyersiinae

17(14) Apterous. Evaporatory area of metathoracic scent gland with a vermiculate pattern of fine ridges (Fig. 21); tarsal segments 3 in number; pulvilli bristlelike (Fig. 22). [Habitus, Fig. 26; body length, about 11 mm] . . . . Tribe Tretocorini, Genus *Tretocoris*

– Macropterous. Evaporatory area of metathoracic scent gland not ridged; tarsal segments 2 in number; pulvilli spatulate (Fig. 23). [Body covered with numerous broad, flattened granules; habitus, Fig. 27; body length, about 4.5-7.2 mm] . . . . Tribe Chinamyersiini, Genus *Chinamyersia*

Subfamilies Calisiinae, Aradinae

18(13) Scutellum greatly enlarged, covering wings and abdomen except double-edged connexivum (Fig. 24); body tuberculate (Fig. 24), especially along margins; forewings membranous, except for thickened costal margin (Fig. 43) exposed along basal half of scutellum. [Habitus, Fig. 24; body length, about 2.8-3.5 mm] . . . . **Subfamily Calisiinae**, Genus *Calisius*

– Scutellum not greatly enlarged, leaving forewings and single-edged connexivum broadly exposed (Fig. 25); body not tuberculate; forewings of the standard hemelytral type (with corium and membrane). [Habitus, Fig. 25; body length, about 5.0-6.5 mm] . . . . **Subfamily Aradinae**, Genus *Aradus*

Overview of genera

Subfamily Calisiinae

Description (New Zealand): **Head**. Genae not large (not produced anteriorly on either side of clypeus, not surpassing its apex). Rostrum short, not reaching beyond hind margin of head; bordered by bucculae at base; arising from an open atrium. Gula with rostral groove. Labrum free (not fused with clypeus). Feeding stylets coiled into clockwise circle. **Thorax**. Metathoracic scent gland openings indistinct, without well-developed evaporatory area. Pretarsi with spatulate pulvilli laminate apically. **Abdomen**. Posterior margin of tergites III-V straight or nearly so. Dorsal abdominal scent gland openings (or scars thereof) equally developed. Pattern of glabrous areas 2:1:1 (dorsal); 2:2:1 (ventral). Paratergites of abdominal segment VIII of male well developed, projecting as lobes on each side of pygophore.

Genus *Calisius* Stål 1860 (Figs 24, 43)

Synonymy (Larivière & Larochelle 2004: 51).

Description (New Zealand): Body oblong-oval (usually tuberculate along margins), with rounded abdomen, about 2.8-3.5

mm long. **Head**. Clypeus bulbous. **Thorax**. Scutellum greatly enlarged, apically rounded, covering wings and abdomen except connexivum (usually with three tubercles near posterior margin of connexival segments). Submacropterous; forewings almost entirely membranous, completely hidden by scutellum (except for thickened costal margins exposed along basal half of scutellum). **Abdomen**. Connexivum broadly exposed, double-edged. Dorsal abdominal scent gland openings (or scars thereof) three in number, equally developed and equally spaced along posterior margin of tergites III, IV, V. Other characters as for subfamily.

Included species: About 100 circumtropical species; *Calisius zealandicus* PENDERGRAST 1968 (endemic to New Zealand).

References: KORMILEV 1958 (Australian region, key, Neotropical region, taxonomy). USINGER & MATSUDA 1959 (classification, key to species, taxonomy, world). KORMILEV 1963 (Australia, key, morphology, taxonomy), 1966 (Australia, distribution, key, taxonomy), 1967a (Australia, key to species, South Pacific, taxonomy). PENDERGRAST 1968 (New Zealand, taxonomy; *C. zealandicus*). KORMILEV 1986 (keyed, taxonomy, world). FROESCHNER 1992 (taxonomy). LARIVIÈRE & LAROCHELLE 2004: 51 (catalogue, New Zealand).

Notes: *Calisius* is the only representative of the subfamily Calisiinae in New Zealand. See also under *Aradus*. LARIVIÈRE & LAROCHELLE (2004) erroneously interpreted the enlarged scutellum of *Calisius* as being fused hemelytra.

Subfamily Aradinae

Description (New Zealand): **Head**. Genae not large (not produced anteriorly on either side of clypeus, not surpassing its apex). Rostrum long, reaching beyond hind margin of head; bordered by bucculae at base; arising from an open atrium. Gula with rostral groove. Labrum free (not fused with clypeus). Feeding stylets coiled into a clockwise circle. **Thorax**. Metathoracic scent gland openings inconspicuous, without well-developed evaporatory area. Pretarsi without pulvilli. **Abdomen**. Posterior margin of tergites III-V straight or nearly so. Dorsal abdominal scent gland openings (or scars thereof) equally developed. Pattern of glabrous areas 2:2:1 (dorsal; ventral). Paratergites of abdominal segment VIII of male well developed, projecting as lobes on each side of pygophore.

Genus *Aradus* FABRICIUS 1803 (Fig. 25)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 50).

Description (New Zealand): Body elongate oval, about 5.0-6.5 mm long. **Head**. Clypeus bulbous. **Thorax**. Scutellum elongate, triangular. Submacropterous-macropterous; hemelytra (forewings) variously developed, completely exposed. Metathoracic scent gland openings small, forming a simple hole. **Abdomen**. Connexivum usually broadly exposed and single-edged. Dorsal abdominal scent gland openings (or scars thereof) three in number, equally developed and equally spaced along posterior margin of tergites III, IV, V. Other characters as for subfamily.

Included species: Over 200 species worldwide, mostly from the Holarctic Region; *Aradus australis* ERICHSON 1842 (native although not endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, taxonomy, world). KORMILEV 1966 (Australia, distribution, key, taxonomy). PENDERGRAST 1968 (New Zealand, taxonomy; *A. australis*). LARIVIÈRE & LAROCHELLE 2004: 50-51 (catalogue, New Zealand).

Notes: Because the subfamilies Aradinae and Calisiinae are hypothesized to be sister groups and because both subfamilies only have a single genus in New Zealand, the description of *Aradus* in this study is most directly comparative to that of *Calisius*. According to USINGER & MATSUDA (1959), the pattern of glabrous area of Aradinae is 2:1:1 (dorsal), 2:2:1 (ventral). All adult specimens of *Aradus australis* examined for this study had a dorsal pattern of 2:1:1, with the most inner areas barely visible. The ventral pattern of 2:2:1 was more difficult to observe, especially the connexival and midlateral areas which often appeared to be 1:1, perhaps because of the relatively small size of this species and the ventral areas being less obvious in the adult stage.

Subfamily Chinamyersiinae

Description (New Zealand): **Head**. Genae not large (not produced anteriorly on either side of clypeus, not surpassing its apex). Rostrum long, reaching beyond hind margin of head; bordered by bucculae at base; arising from an open atrium. Gula with (*Chinamyersia*) or without (*Tretocoris*) rostral groove. Labrum free (not fused with clypeus). Feeding stylets coiled into a figure of eight (*Chinamyersia*) or into a clockwise circle (*Tretocoris*). **Thorax**. Metathoracic scent gland openings conspicuous, with well-developed evaporatory area. Pretarsi with spatulate pulvilli not laminate apically (*Chinamyersia*) or bristlelike pulvilli (*Tretocoris*). **Abdomen**. Posterior margin of tergites III-V distinctly bent backwards (*Chinamyersia*), or, straight or nearly so (*Tretocoris*). Dorsal abdominal scent gland openings (or scars thereof) equally developed. Pattern of glabrous areas 1:1:1 (*Chinamyersia*) or 2:1:1 (*Tretocoris*) (dorsal); 1:2:1 (ventral). Paratergites of abdominal segment VIII of male well developed, projecting as lobes on each side of pygophore.

Tribe Tretocorini

Genus *Tretocoris* USINGER & MATSUDA 1959 (Fig. 26)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 54).

Description: Body suboval to subquadrate, attenuate anteriorly, with subrectangular abdomen, about 11 mm long, covered with short hairs and surface somewhat granular (not covered with numerous broad, flattened granules as in *Chinamyersia*). **Head**. Eyes stalked. Rostral groove absent; feeding stylets when retracted coiled into a simple circle. **Thorax**. Notal lobes scalloped; pronotum without blunt spine on either side of collar; scutellum in the form of a semicircular slightly depressed plate in the middle of the mesonotum, not reaching beyond posterior margin of metanotum. Metathoracic scent gland openings present, conspicuous, with a raised ridge curved at apex (without a seta); evaporatory area with a vermiculate pattern of fine ridges. Apterous. Legs without conspicuous spines or processes; front and middle trochanters fused with femur; tarsal segments three in number; pretarsi with bristlelike pulvilli. **Abdomen**. Dorsal abdominal scent gland openings (or scars thereof) three in number, equally developed and equally spaced along the posterior margin of tergites III, IV, V; the latter straight or nearly so. Abdominal spiracles 5-6 ventral (2-3 lateral; 4-7, ventral; 8, lateral). Pattern of glabrous areas 2:1:1 (dorsal); 1:2:1 (ventral). Other characters as for subfamily.

Included species: A single species, *Tretocoris grandis* USINGER & MATSUDA 1959 (endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). MONTEITH 1966, 1969a (relationships), 1980 (keyed, relationships). LARIVIÈRE & LAROCHELLE 2004: 54 (catalogue, New Zealand).

Tribe Chinamyersiini

Genus *Chinamyersia* USINGER 1943 (Fig. 27)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 54).

Description: Body suboval to subquadrate, attenuate anteriorly, with rounded abdomen, about 4.5-7.2 mm long, without short hairs but covered with numerous broad, flattened granules. **Head**. Eyes normally developed, not stalked. Rostral groove present; feeding stylets when retracted coiled into a figure of eight. **Thorax**. Notal lobes entire (not scalloped); pronotum with blunt anterior spine on each side of collar; scutellum subtriangular to subpentagonal, reaching beyond posterior margin of metanotum. Metathoracic scent gland openings present, conspicuous, with a raised ridge curved at apex (without a seta); evaporatory area without a vermiculate pattern of fine ridges. Macropterous. Legs without conspicuous spines or processes; front and middle trochanters fused with femur; tarsal segments 2 in number; pretarsi with spatulate pulvilli not laminate apically. **Abdomen**. Dorsal abdominal scent gland openings (or scars thereof) three in number, equally developed and equally spaced along the posterior margin of tergites III, IV, V; the latter distinctly bent backwards. Abdominal spiracles 5-6 dorsal (2-3 ventral; 4-6 dorsal; 7-8 ventral). Pattern of glabrous areas 1:1:1 (dorsal); 1:2:1 (ventral). Other characters as for subfamily.

Included species: Two species, *Chinamyersia cinerea* (MYERS & CHINA 1928) and *C. viridis* (MYERS & CHINA 1928) (both endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). MONTEITH 1980 (keyed, relationships). LARIVIÈRE & LAROCHELLE 2004: 54 (catalogue, New Zealand).

Note: USINGER & MATSUDA (1959) reported "legs with unusual spines or processes". The only unusual feature that could be observed is a granular pattern on the integument of the femora, very similar to although somewhat more spiky than that covering the remainder of the body, but nothing that could be described as spines or processes.

Subfamily Prosympiestinae

Description (New Zealand): **Head**. Genae not large (not produced anteriorly on either side of clypeus, not surpassing its apex). Rostrum long, reaching beyond hind margin of head; bordered by bucculae at base; arising from an open atrium. Gula without rostral groove. Labrum fused with clypeus. Feeding stylets coiled into an anticlockwise circle. **Thorax**. Metathoracic scent gland openings conspicuous, with well-developed evaporatory area. Pretarsi with spatulate pulvilli not laminate apically. **Abdomen**. Posterior margin of tergites III-V distinctly bent backwards. Dorsal abdominal scent gland openings (or scars thereof) equally developed. Pattern of glabrous areas 2:1:1 (dorsal); 2:2:1 (ventral). Paratergites of abdominal segment VIII of male inconspicuous, not projecting as lobes on each side of pygophore.

Tribe Prosympiestini

Genus *Adenocoris* USINGER & MATSUDA 1959 (Fig. 28)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 57).

Description: Body suboval, about 4.7-6.5 mm long. **Head**. Antennae inserted on spine-like tubercles; third segment not distinctly shorter than all other segments. Rostrum reaching between front coxae. **Thorax**. Pronotum with lateral margins arcuate, more or less produced laterally at middle; anterolateral angles rounded, not produced anteriorly. Micropterous; hemelytra reduced to short pads not extending beyond apex of scutellum. Metathoracic scent gland openings with a long, curved seta in middle and not directly connecting to channel of evaporatory area, the latter strongly developed (occupying a considerable portion of metapleuron and extending anteriorly and laterally to lateral margin). **Abdomen**. Tergites I, II well separated; III-VI fused, their posterior margin indistinct. Dorsal abdominal scent glands (or scars thereof) three in number; first opening displaced posteriorly to middle or posterior margin of tergite IV; all openings equally developed. Other characters as for subfamily.

Included species: Two species, *Adenocoris brachypterus* USINGER & MATSUDA 1959 and *A. spiniventris* USINGER & MATSUDA 1959 (both endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed as genus, key to species, taxonomy). KIRMAN 1985b (keyed). LARIVIÈRE & LAROCHELLE 2004: 57 (catalogue, New Zealand).

Genus *Mesadenocoris* KIRMAN 1985 (Fig. 29)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 57).

Description: Body oval, with broadly rounded abdomen, about 5.5-8.0 mm long. **Head**. Antennae inserted on spine-like tubercles; third segment distinctly shorter than all other segments. Rostrum reaching or just surpassing posterior margin of head. **Thorax**. Pronotum with lateral margins straight or nearly so; anterolateral angles subacute, produced anteriorly. Micropterous; hemelytra reduced to short pads not extending beyond apex of scutellum. Metathoracic scent gland openings with a long, curved seta in middle and not directly connecting to channel of evaporatory area, the latter strongly developed (occupying a considerable part of metapleuron and extending anteriorly and laterally to lateral margin). **Abdomen**. Tergites I, II well separated; III-VI more or less fused, their posterior margin mostly indistinct. Dorsal abdominal scent glands (or scars thereof) three in number; first opening displaced posteriorly to middle or posterior margin of tergite IV; all openings equally developed. Other characters as for subfamily.

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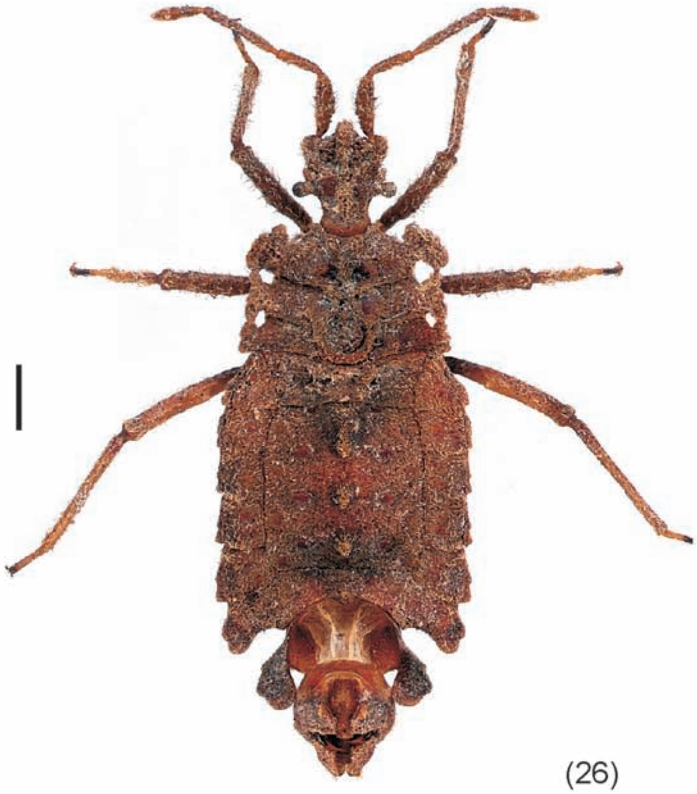

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Fig. 24: *Calisius zealandicus* (Calisiinae), female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)
Fig. 25: *Aradus australis* (Aradinae), female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière).
Fig. 26: *Tretocoris grandis* (Chinamyersiinae, Tretocorini), male, dorsal view. Scale bar = 1 mm. (Photo: B.E. Rhode)
Fig. 27: *Chinamyersia cinerea* (Chinamyersiinae, Chinamyersiini), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)

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Fig. 28: *Adenocoris spiniventris* (Prosympiestinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)
Fig. 29: *Mesadenocoris robustus* (Prosympiestinae), male holotype, dorsal view. Scale bar = 1 mm. (Photo: B.E. Rhode)
Fig. 30: *Neadenocoris spinicornis* (Prosympiestinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)
Fig. 31: *Isodermus tenuicornis* (Isoderminae), female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)

Included species: A single species, *Mesadenocoris robustus* KIRMAN 1985 (endemic to New Zealand).

References: KIRMAN 1985b (keyed, taxonomy). LARIVIÈRE & LAROCHELLE 2004: 57 (catalogue, New Zealand).

Note: Characters of the metathoracic scent gland openings, evaporatory area, and abdominal tergites suggest this genus may be more closely related to *Adenocoris* than to *Neadenocoris*, although it shares a number of other features with both genera.

Genus *Neadenocoris* USINGER & MATSUDA 1959 (Fig. 30)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 57).

Description: Body subtriangular, with broad abdomen, about 3.0-4.5 mm long. **Head**. Antennae inserted on cylindrical tubercles (sometimes slightly concave apically, but not distinctly spinous); third segment not distinctly shorter than all other segments. Rostrum reaching or just surpassing posterior margin of head. **Thorax**. Pronotum with lateral margins straight or nearly so; anterolateral angles subacute, produced anteriorly. Micropterous; hemelytra reduced to short pads not extending beyond apex of scutellum. Metathoracic scent gland openings with a long, curved seta in middle and directly connecting to channel of evaporatory area, the latter moderately developed (occupying a lesser portion of metapleuron and extending anteriorly although not laterally to lateral margin). **Abdomen**. Tergites all clearly separated; posterior margin of tergites III-VI strongly sinuate on either side of scent gland openings. Dorsal abdominal scent glands (or scars thereof) three in number; first opening displaced posteriorly to middle or posterior margin of tergite IV; all openings usually equally developed (third one sometimes slightly smaller). Other characters as for subfamily.

Included species: Six species, *Neadenocoris abdominalis* USINGER & MATSUDA 1959, *N. acutus* USINGER & MATSUDA 1959, *N. glaber* USINGER & MATSUDA 1959, *N. ovatus* USINGER & MATSUDA 1959, *N. reflexus* USINGER & MATSUDA 1959, and *N. spinicornis* USINGER & MATSUDA 1959 (all endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed as genus, key to species, taxonomy). KIRMAN 1985b (keyed). LARIVIÈRE & LAROCHELLE 2004: 57-59 (catalogue, New Zealand).

Note: Examination of Prosympiestinae material from the North Island suggests additional undescribed species that may belong to this genus or to a closely related undescribed genus.

Subfamily Isoderminae

Description (New Zealand): **Head**. Genae not large (not produced anteriorly on either side of clypeus, not surpassing its apex). Rostrum long, reaching beyond hind margin of head; entirely exposed at base (not usually bordered by bucculae or arising from an atrium). Gula without rostral groove. Labrum fused with clypeus. Feeding stylets coiled into an anticlockwise circle. **Thorax**. Metathoracic scent gland openings conspicuous, with well-developed evaporatory area. Pretarsi with spatulate pulvilli laminate apically. **Abdomen**. Posterior margin of tergites III-V straight or nearly so. Dorsal abdominal scent gland openings (or scars thereof) equally developed. Pattern of glabrous areas 2:1:1 (dorsal); 2:2:1 (ventral). Paratergites of abdominal segment VIII of male inconspicuous, not projecting as lobes on each side of pygophore.

Note: In Isoderminae the rostrum usually arises at or near the apex of the clypeus from an anteroventral extension of its surface. In the New Zealand species *Isodermus maculosus* PENDERGRAST 1965, the rostrum arises in a more backward position, almost levelled with the antennal base, from what appears to be a small atrium bordered by slightly raised bucculae.

Genus *Isodermus* ERICHSON 1842 (Fig. 31)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 54).

Description (New Zealand): Body elongate, almost parallel-sided, about 4.5-6.5 mm long. **Head.** Juga well developed, reaching about middle of clypeus. **Thorax**. Scutellum triangular. Macropterous; hemelytra with line of weakness at level of apex of scutellum, often broken off at this level. Prosternum forming a distinctly elevated plate between front coxae. Metathoracic scent gland openings small but distinct, located just behind middle coxae, with evaporatory channel reaching to lateral margin of metapleuron. Legs short; trochanters distinct (not fused with femur); femora inflated and spined. **Abdomen**. Dorsal abdominal scent gland openings (or scars thereof) three in number, equally developed and equally spaced along posterior margin of tergites III, IV, V. Abdominal spiracles sublateral (almost ventral). Other characters as for subfamily.

Included species: Six species from Chile, New Zealand, continental Australia, and Tasmania; *Isodermus crassicornis* USINGER & MATSUDA 1959, *I. maculosus* PENDERGRAST 1965 and *I. tenuicornis* USINGER & MATSUDA 1959 (all endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, key to species, taxonomy). PENDERGRAST 1965b (key to species, New Zealand, taxonomy). KORMILEV 1966 (Australia, distribution, taxonomy). HEISS 1981 (Australia, distribution, morphology, New Zealand, South America). LARIVIÈRE & LAROCHELLE 2004: 54-55 (catalogue, New Zealand).

Note: In *Isodermus* both sexes shed their hemelytra along a line of weakness at the level of the apex of scutellum – a behaviour only found elsewhere in gerromorphan Heteroptera (SCHUH & SLATER 1995). Museum specimens often have the apex of the hemelytra broken off, which may mislead some people to think they represent brachypterous forms.

Subfamily Aneurinae

Description (New Zealand): **Head**. Genae large (produced anteriorly on either side of clypeus, nearly reaching or surpassing its apex to form a cleft or emarginate anterior margin of head). Rostrum short, not reaching beyond hind margin of head; bordered by bucculae at base; arising from an open atrium. Gula without rostral groove. Labrum fused with clypeus. Feeding stylets coiled into an anticlockwise circle. **Thorax**. Metathoracic scent gland openings inconspicuous, without well-developed evaporatory area. Pretarsi with spatulate pulvilli not laminate apically. **Abdomen**. Posterior margin of tergites III-V straight or nearly so. Dorsal abdominal scent glands with first opening (or scar thereof) more developed than second and third. Pattern of glabrous areas 2:2:1 (dorsal; ventral). Paratergites of abdominal segment VIII of male well developed, projecting as lobes on each side of pygophore.

Genus *Aneuraptera* USINGER & MATSUDA 1959 (Fig. 32)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 48).

Description: Body broadly oval, about 5 mm long. **Head**. Genae produced anteriorly, nearly reaching but not surpassing apex of clypeus, forming a narrowly convex anterior margin of head (genae only visible dorsally as extremely thin prolongations parallel to the clypeus). Juga more or less distinct on either side of clypeus, only reaching near its base. **Thorax**. Scutellum in the form of a short, posteriorly arcuate elevation in the middle of the mesonotum. Micropterous; hemelytra reduced to short lateral pads (tergal disc of abdomen completely exposed). Femora subcylindrical. **Abdomen**. Connexivum delimited by deep longitudinal sutures dorsally and ventrally, and with sublateral folds dorsally. Ventral surface feebly convex; sternites IV, V, VI without a distinct transverse carina along anterior margin. Other characters as for subfamily.

Included species: A single species, *Aneuraptera cimiciformis* USINGER & MATSUDA 1959 (endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). PENDERGRAST 1965a (taxonomy). LARIVIÈRE & LAROCHELLE 2004: 48-49 (catalogue, New Zealand).

Note: In this genus, the degree of development of the genae on either side of the clypeus can be more easily observed in ventrolateral view than in dorsal view.

Genus *Aneurus* CURTIS 1825

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 49).

Description: Body elongate oval, about 5 mm long. **Head**. Genae produced anteriorly, reaching or surpassing apex of clypeus, forming cleft or emarginate anterior margin of head (genae clearly visible dorsally). Juga well developed on either side of clypeus, reaching about half its length. **Thorax**.

Scutellum subtriangular, broadly rounded apically. Macropterous or submacropterous; hemelytra usually well developed (tergal disc of abdomen barely exposed). Femora incrassate. **Abdomen**. Connexivum delimited by deep longitudinal sutures dorsally only, without sublateral folds dorsally. Ventral surface flattened, plate-like; sternites IV, V, VI with a distinct transverse carina along anterior margin. Other characters as for subfamily.

Included species: Over 100 species from all major geographic regions.

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). KORMILEV 1965 (Australia, key to species), 1966 (Australia, distribution, key, taxonomy), 1967b (key to species, South America). KORMILEV & HEISS 1973 (key to species, Oriental Region). HEISS 1998 (New Zealand, revision). LARIVIÈRE & LAROCHELLE 2004: 49-50 (catalogue, New Zealand).

Subgenus *Aneurodellus* HEISS 1998 (Fig. 33)

Description: (HEISS 1998: 30-31).

Included species: Six species, *Aneurus* (*A.*) *brevipennis* HEISS 1998, *A.* (*A.*) *brouni* WHITE 1876, *A.* (*A.*) *maoricus* HEISS 1998, *A.* (*A.*) *prominens* PENDERGRAST 1965, *A.* (*A.*) *salmoni* PENDERGRAST 1965, and *A.* (*A.*) *zealandensis* HEISS 1998 (all endemic to New Zealand).

References: PENDERGRAST 1965a (taxonomy; as *Aneurus*). KORMILEV 1968a (distribution, Pacific, taxonomy). HEISS 1998 (key to species, revision). LARIVIÈRE & LAROCHELLE 2004: 49-50 (catalogue, New Zealand).

Note: HEISS (1998) gave a list of characters distinguishing the subgenus *Aneurodellus* from the Palearctic *Aneurus* sensu stricto and *Aneurodes* to which *Aneurodellus* appears most closely related by the presence of an area of glabrous cuticle (contergite) on the inner side on the fused connexival segments II+III.

Subfamily Carventinae

Description: (New Zealand). **Head**. Genae large (produced anteriorly on either side of clypeus, nearly reaching or surpassing its apex to form a cleft or emarginate anterior margin of head). Rostrum short, not reaching beyond hind margin of head; bordered by bucculae at base; arising from a closed or open (*Acaraptera*, *Lissaptera*) atrium. Gula with rostral groove. Labrum fused with clypeus. Feeding stylets coiled into an anticlockwise circle. **Thorax**. Metathoracic scent gland openings inconspicuous, without well-developed evaporatory area. Pretarsi with spatulate pulvilli not laminate apically. **Abdomen**. Posterior margin of tergites III-V distinctly bent backwards. Dorsal abdominal scent glands with first opening (or scar thereof) more developed than second and third. Pattern of glabrous areas 2:1:1 (dorsal, except 2:2:1 in *Acaraptera* and *Lissaptera*); 2:2:1 (ventral, except 2:1:1 in *Leuraptera*). Paratergites of abdominal segment VIII of male well developed, projecting as lobes on each side of pygophore.

Note: All Carventinae have the opening (or visible scar) of the first dorsal abdominal scent gland displaced posteriorly. As elsewhere in the world, New Zealand Carventinae have the body covered with pale incrustation patterns more or less obscuring the integument. It is necessary to clear specimens of such incrustations before examination, otherwise, important diagnostic features, especially the shape and limits of body sclerites, may be obscured. Specimens collected in ethanol can be left to dry for a few minutes under a lamp and then cleaned under the microscope, before mounting, using the tip of a fine entomological pin or needle to scratch off the incrustations. It is also possible to clean already mounted specimens using the same method after soaking them in hot ethanol for about 30 minutes.

Group I (of USINGER & MATSUDA 1959)

Notes: The main diagnostic characters of this group are the closed rostral atrium and the fused connexival segments II + III not extending forwards to posterior angles of pronotum. The five New Zealand genera are arranged alphabetically within this group which is one of two evolutionary lines hypothesized by Usinger & Matsuda (1959) for New Zealand genera "from the *Carventus*-like ancestor … the *Carventaptera*, *Neocarventus*, *Leuraptera* line."

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Fig. 32: *Aneuraptera cimiciformis* (Aneurinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)
Fig. 33: *Aneurus* (*Aneurodellus*) *zealandensis* (Aneurinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)
Fig. 34: *Carventaptera spinifera* (Carventinae), female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)
Fig. 35: *Clavaptera ornata* (Carventinae), female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. Larivière)

Genus *Carventaptera* Usinger & Matsuda 1959 (Fig. 34)

Synonymy (Larivière & Larochelle 2004: 52).

Description: Body subrectangular, about 4.0-5.0 mm long. **Head**. Eyes rather large in relation to head. Postocular spines strongly developed, narrowly acutely angled, extending laterally to or slightly beyond outer margins of eyes. Rostrum arising from a closed atrium. **Thorax**. Pronotum with a double-ring collar distinctly set off from the anterior margin, with lateral tubercles but lacking posteriorly directed subtriangular sclerite. Mesonotum and metanotum distinctly separated; medial region of mesonotum produced backwards as a subtriangular lobe reaching 2/3-3/4 length (not reaching posterior margin) of metanotum; lateral margins of metanotum not flaring posteriorly into projections. Sutures between notal sclerites distinct but not deep. Apterous. **Abdomen**. Tergites I, II separated from metanotum by a distinct suture throughout; fused to each other and elevated anteriorly near middle. Tergal disc with segments III-VI completely fused, with a distinct median longitudinal elevation with 2 median tumescent tubercles fused at middle, bearing scent gland openings. Dorsal abdominal scent glands (or scars thereof) three in number; first opening moderately developed, displaced posteriorly to middle or posterior margin of tergite IV; second very small; third lacking. Fused connexival segments II + III not extending forwards to posterior angles of pronotum. Only spiracles 5-7 lateral and visible from above. Patterns of glabrous areas 2:1:1 (dorsal); 2:2:1(ventral). Other characters as for subfamily.

Included species: A single species, *Carventaptera spinifera* Usinger & Matsuda 1959 (endemic to New Zealand).

References: Usinger & Matsuda 1959 (classification, keyed, taxonomy). Kirman 1989a (keyed). Larivière & Larochelle 2004: 52 (catalogue, New Zealand).

Genus *Clavaptera* Kirman 1985 (Fig. 35)

Synonymy (Larivière & Larochelle 2004: 52).

Description: Body subrectangular, about 3.0-3.5 mm long. **Head**. Eyes rather small in relation to head. Postocular spines slightly developed, obtusely angled, extending laterally almost to outer margins of eyes. Rostrum arising from a closed atrium. **Thorax**. Pronotum with a double-ring collar distinctly set off from the anterior margin, with lateral tubercles but lacking posteriorly directed subtriangular sclerite. Mesonotum and metanotum distinctly separated, except at middle where fused into a smooth hexagonal tumescence (sometimes elliptical in female) extending from anterior margin of mesonotum to posterior margin of metanotum; lateral margins of metanotum flaring posteriorly into more or less acutely rounded projections (more developed in males). Sutures between notal sclerites very deep. Apterous. **Abdomen**. Tergites I, II separated from metanotum and from each other by a distinct suture throughout; elevated anteriorly; a rather thick median longitudinal carina cutting across both tergites; two anterolateral pits (one on each side) behind posterior margin of metanotum (as in *Neocarventus*). Tergal disc with segments III-VI completely fused, gradually elevated medially into a moderate longitudinal elevation (not delimited by faint lateral margins) bearing scent gland openings. Dorsal abdominal scent glands (or scars thereof) three in number; first opening, large, displaced posteriorly to middle or posterior margin of tergite IV; second and third barely distinct. Fused connexival segments II + III not extending forwards to posterior angles of pronotum. Only spiracles 3-7 lateral and visible from above. Pattern of glabrous areas 2:1:1 (dorsal); 2:2:1 (ventral). Other characters as for subfamily.

Included species: A single species, *Clavaptera ornata* Kirman 1985 (endemic to New Zealand).

References: Kirman 1985a (taxonomy), 1989a (keyed). Larivière & Larochelle 2004: 52 (catalogue, New Zealand).

Genus *Leuraptera* Usinger & Matsuda 1959 (Fig. 36)

Synonymy (Larivière & Larochelle 2004: 52).

Description: Body oval, about 3.7-4.8 mm long. **Head**. Eyes very small in relation to head. Postocular spines strongly developed, acutely angled, extending laterally to or slightly beyond outer margins of eyes. Rostrum arising from a closed atrium. **Tho-**

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Fig. 36: *Leuraptera zealandica* (Carventinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)
Fig. 37: *Modicarventus wisei* (Carventinae), female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)
Fig. 38: *Neocarventus angulatus* (Carventinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)
Fig. 39: *Acaraptera wisei* (Carventinae) showing some body surface incrustations, female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)

rax. Pronotum with a double-ring collar distinctly set off from the anterior margin, with lateral tubercles but lacking posteriorly directed subtriangular sclerite. Mesonotum and metanotum distinctly separated; medial region of mesonotum and metanotum separated in two by forward-extended subtriangular median lobe of abdominal base; lateral margins of metanotum not flaring posteriorly into projections. Sutures between notal sclerites distinct but not deep. Apterous. **Abdomen**. Tergites I, II separated from metanotum and from each other by a distinct suture laterally only. Tergal disc with segments III-VI completely fused, usually without (sometimes with faint) median longitudinal elevation (not delimited by faint lateral margins) bearing scent gland openings. Dorsal abdominal scent glands (or scars thereof) three in number; first opening moderately developed, displaced posteriorly to middle or posterior margin of tergite IV; second very small; third evanescent. Fused connexival segments II + III not extending forwards to posterior angles of pronotum. Only spiracles 5-7 lateral and visible from above. Pattern of glabrous areas noticeable although sometimes faint, 2:1:1 (dorsal; ventral). Other characters as for subfamily.

Included species: Two species, *Leuraptera yakasi* HEISS 1990 and *L. zealandica* USINGER & MATSUDA 1959 (both endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). KIRMAN 1989a (keyed). HEISS 1990 (taxonomy; *L. yakasi*). LARIVIÈRE & LAROCHELLE 2004: 52 (catalogue, New Zealand).

Genus *Modicarventus* KIRMAN 1989 (Fig. 37)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 53).

Description: Body broadly pear-shaped to subrectangular, about 2.5-3.5 mm long. **Head**. Eyes rather small in relation to head. Postocular spines barely developed, forming narrowly rounded postocular swellings. Rostrum arising from a closed atrium. **Thorax**. Pronotum with a double-ring collar distinctly set off from the anterior margin, with lateral tubercles and posteriorly directed subtriangular sclerite. Mesonotum and metanotum distinctly separated; medial region of mesonotum produced backwards as a subquadrate to pentagonal lobe reaching posterior margin of metanotum; lateral margins of metanotum not flaring posteriorly into projections as in *Clavaptera* or *Neocarventus*. Sutures between notal sclerites distinct but not deep. Apterous. **Abdomen**. Tergites I, II separated from metanotum by distinct suture throughout; mostly fused to each other, but with trace of a faint suture between the two; a tubercle-bearing median longitudinal groove cutting across both sclerites; two anterolateral slits (as opposed to pits in *Clavaptera* and *Neocarventus*) (one on each side) behind posterior margin of metanotum. Tergal disc with segments III-VI superficially unfused, with well delimited individual sublateral and inner sclerites (4 sublateral and 4 inner sclerites); only slightly elevated at middle into short longitudinal elevation bearing scent gland openings. Dorsal abdominal scent gland openings (or scars thereof) three in number; first opening large, displaced posteriorly slightly behind middle of segment IV; second very small; third lacking. Fused connexival segments II + III not extending forwards to posterior angles of pronotum. Only spiracles 1, 5-7 lateral and visible from above. Pattern of glabrous areas 2:1:1 (dorsal); 2:2:1 (ventral). Other characters as for subfamily.

Included species: A single species, *Modicarventus wisei* KIRMAN 1989 (endemic to New Zealand).

References: KIRMAN 1989a (keyed, taxonomy). LARIVIÈRE & LAROCHELLE 2004: 53 (catalogue, New Zealand).

Genus *Neocarventus* USINGER & MATSUDA 1959 (Fig. 38)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 53).

Description: Body subovate (*N. angulatus*) or subrectangular (*N. uncus*), about 2.5-3.5 mm long. **Head**. Eyes rather large in relation to head. Postocular spines lacking or barely developed, forming narrow postocular swellings (*N. angulatus*) or slightly developed, obtusely angled, nearly extending to outer margins of eyes (*N. uncus*). Rostrum arising from a closed atrium. **Thorax**. Pronotum with a double-ring collar distinctly set off from the anterior margin, with lateral tubercles and posteriorly directed subtriangular sclerite. Mesonotum and metanotum distinctly separated; medial region of mesonotum produced backwards into triangular (*N. angulatus*) or subtriangular (*N. uncus*) lobe reaching posterior margin of metanotum; lateral margins of metanotum flaring posteriorly into more or less acutely rounded projections (more developed in males and in *N. uncus*). Sutures between notal sclerites distinct but not deep. Apterous. **Abdomen**. Tergites I, II separated from metanotum by a distinct suture throughout; separated from each other laterally only (*N. angulatus*) or throughout (*N. uncus*); elevated anteriorly; a rather thick median longitudinal carina cutting across both tergites (as in *Clavaptera*); two anterolateral pits (as in *Clavaptera*) (one on each side) behind posterior margin of metanotum. Tergal disc with segments III-VI completely fused (*N. angulatus*) or in part superficially unfused (*N. uncus*) with well delimited sublateral sclerites and with inner sclerites partly fused with median elevation, the latter gradually elevated towards middle (delimited by lateral margins), bearing scent gland openings. Dorsal abdominal scent gland openings (or scars thereof) three in number; first opening moderately developed, displaced posteriorly to middle or posterior margin of tergite IV; second very small; third lacking. Fused connexival segments II + III not extending forwards to posterior angles of pronotum. Only spiracles 5-7 lateral and visible from above. Pattern of glabrous areas 2:1:1 (dorsal); 2:2:1 (ventral). Other characters as for subfamily.

Included species: Two species, *Neocarventus angulatus* USINGER & MATSUDA 1959 and *N. uncus* KIRMAN 1989 (both endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). KIRMAN 1989a (keyed), 1989b (redescription, taxonomy). LARIVIÈRE & LAROCHELLE 2004: 53 (catalogue, New Zealand).

Note: *Neocarventus* is morphologically closer to *Clavaptera* than to *Modicarventus*.

Group II (of USINGER & MATSUDA 1959)

Notes: The main diagnostic characters of this group are the open rostral atrium and the fused connexival segments II + III extending forwards to posterior angles of pronotum. The two New Zealand genera (*Acaraptera* and *Lissaptera*) are arranged alphabetically within this group which is the second evolutionary line hypothesized by USINGER & MATSUDA (1959) to include New Zealand genera "the *Acaraptera-Chelonaptera* line [*lapsus*]" [= *Acaraptera-Biroana* line (Monteith pers. comm.)] and thought to be further removed from a *Carventus*-like ancestor than Group I. Further comments on Group II may be found in MONTEITH (1967). The genus *Nesiaptera* (islands of Samoa and Fiji) is the closest relative of *Acaraptera* and *Lissaptera*.

Genus *Acaraptera* USINGER & MATSUDA 1959 (Fig. 39)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 51).

Description: Body pear-shaped, about 2.5-4.5 mm long. **Head**. Eyes rather large in relation to head. Postocular spines moderately to barely developed, usually quadrate, extending laterally almost to outer margins of eyes, or, sometimes forming narrowly rounded postocular swellings. Rostrum arising from an open atrium. **Thorax**. Pronotum with a single-ring collar barely set off from the anterior margin, without tubercles or posteriorly directed subtriangular sclerite. Mesonotum and metanotum distinctly separated; medial region of mesonotum produced backwards as a subtriangular lobe reaching into anterior 1/3 of metanotum; lateral margins of metanotum not flaring posteriorly into projections. Sutures between notal sclerites distinct but not deep. Apterous. **Abdomen**. Tergites I, II separated from metanotum by a distinct suture throughout; fused to each other (*A. myersi*) or fused only laterally, separated by a distinct suture medially (*A. waipouensis*). Tergal disc with segments III-VI completely fused, with a distinct median longitudinal elevation (delimited by faint lateral margins) bearing scent gland openings. Dorsal abdominal scent gland openings (or scars thereof) three in number; first opening distinct, large, displaced posteriorly to middle or posterior margin of tergite IV; second smaller; third evanescent or lacking. Fused connexival segments II + III extending forwards to posterior angles of pronotum. Spiracles lateral, all visible from above. Pattern of glabrous areas 2:2:1 (dorsal; ventral). Other characters as for subfamily.

Included species: Five described species – Lord Howe Island (2), New Zealand (2), Solomon Islands (1); also two undescribed species from Norfolk Island (1) and New Caledonia (1) (Monteith pers. comm.); *Acaraptera myersi* USINGER & MATSUDA 1959 and *A. waipouensis* HEISS 1990 (both endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). KORMILEV 1966 (Australia, distribution, New Zealand, sexual dimorphism, taxonomy). MONTEITH 1967 (distribution, morphology). KORMILEV 1968b (distribution, taxonomy). HEISS 1990 (taxonomy). LARIVIÈRE & LAROCHELLE 2004: 51 (catalogue, New Zealand).

Note: USINGER & MATSUDA (1959) described three subgenera, *Acaraptera*, *Lissaptera*, and *Nesiaptera*, that were elevated to generic status by KORMILEV & FROESCHNER (1987).

Genus *Lissaptera* USINGER & MATSUDA 1959 (Fig. 40)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 52).

Description: Body pear-shaped, about 2.5-4.5 mm long. **Head**. Eyes rather large in relation to head. Postocular spines barely to moderately developed, usually forming narrowly rounded postocular swellings, or, sometimes more quadrate, extending laterally almost to outer margins of eyes. Rostrum arising from an open atrium. **Thorax**. Pronotum with a single-ring collar barely set off from the anterior margin, without tubercles or posteriorly directed subtriangular sclerite. Mesonotum and metanotum completely fused, forming a smooth uninterrupted plate; lateral margins of metanotum not flaring posteriorly into projections. Sutures between notal sclerites distinct but not deep. Apterous. **Abdomen**. Tergites I, II partly separated from metanotum by a very short suture medially; completely fused to each other. Tergal disc with segments III-VI completely fused, with or without a slight median longitudinal elevation (not delimited by faint lateral margins) bearing scent gland openings. Dorsal abdominal scent gland openings (or scars thereof) three in number; first opening distinct, large, displaced posteriorly to middle or posterior margin of tergite IV; second very small; third evanescent or lacking. Fused connexival segments II + III extending forwards to posterior angles of pronotum. Spiracles lateral, all visible from above. Pattern of glabrous areas 2:2:1 (dorsal; ventral). Other characters as for subfamily.

Included species: Two species from Lord Howe Island and New Zealand; *Lissaptera completa* (USINGER & MATSUDA 1959) (endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy; as subgenus of *Acaraptera*). KORMILEV 1966 (Australia, distribution, New Zealand, sexual dimorphism, taxonomy). KORMILEV 1968b (distribution, taxonomy). LARIVIÈRE & LAROCHELLE 2004: 52-53 (catalogue, New Zealand).

Subfamily Mezirinae

Description (New Zealand): **Head**. Genae large (produced anteriorly on either side of clypeus, nearly reaching or surpassing its apex to form a cleft or emarginate anterior margin on head). Rostrum short, not reaching beyond hind margin of head (*Woodwardiessa*), or, sometimes longer, reaching beyond hind margin (*Ctenoneurus*); bordered by bucculae at base; arising from a closed (*Ctenoneurus*) or open (*Woodwardiessa*) atrium. Gula with rostral groove. Labrum fused with clypeus. Feeding stylets coiled into an anticlockwise circle. **Thorax**. Metathoracic scent gland openings conspicuous, with well-developed evaporatory area. Pretarsi with spatulate pulvilli not laminate apically. **Abdomen**. Posterior margin of tergites III-V distinctly bent backwards. Dorsal abdominal scent glands with first opening (or scar thereof) more developed than second and third. Pattern of glabrous areas 2:2:1 (dorsal, ventral). Paratergites of abdominal segment VIII of male well developed, projecting as lobes on each side of pygophore.

Notes: Mezirinae lack the body surface incrustations found in Carventinae, but they are often covered with clinging debris. This is especially true of ground-dwelling apterous or micropterous species (e.g., *Woodwardiessa quadrata*), which need to be cleaned before examination. Specimens col-


(40)


(41)


(42)


(43)

Fig. 40: *Lissaptera completa* (Carventinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)
Fig. 41: *Ctenoneurus hochstetteri* (Mezirinae), male, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)
Fig. 42: *Woodwardiessa quadrata* (Mezirinae), female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)
Fig. 43: *Calisius zealandicus* (Calisiinae) with extended wings, female, dorsal view. Scale bar = 1 mm. (Photo: M.-C. LARIVIÈRE)

lected in ethanol can be brushed under the microscope, before mounting, using a fine art brush that has been cut very short at the tip (see MONTEITH 1997). It is also possible to clean already mounted specimens with the same method after soaking them in hot ethanol for about 30 minutes.

Genus *Ctenoneurus* BERGROTH 1887 (Fig. 41)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 55).

Description (New Zealand): Body elongate, subparallel, nearly glabrous, about 6.0-9.0 mm long. **Head**. Eyes normally developed, not stalked as in *Woodwardiessa*. Rostrum arising fom a closed atrium (nearly closed slit-like area of bucculae), extending beyond limits of rostral groove and sometimes onto prosternum. **Thorax**. Anterolateral angles of pronotum obtusely rounded, not produced anteriorly. Scutellum subtriangular, as long or a little longer than pronotum, with prominent spines at basal angles extending forwards over posterior margin of pronotum. Macropterous; hemelytra with fully developed membranes, extending posteriorly onto abdominal tergites VI-VII. Metathoracic scent gland openings conspicuous, located just behind middle coxae, with evaporatory channel reaching to lateral margin of metapleuron. Legs with trochanters distinct (not fused to femur); femora moderately inflated, without spines. **Abdomen:** Tergal disc mostly concealed beneath wings, flattish, smooth and glabrous. Dorsal abdominal scent gland openings (or scars thereof) three in number, not equally developed or spaced along the posterior margin of tergites III, IV, V (first opening large, usually strongly displaced posteriorly to middle or posterior margin of tergite IV; second rarely well developed; third obsolescent). Sternites IV, V, VI with a more or less developed transverse carina along anterior margin. Other characters as for subfamily.

Included species: Over 40 species from the Neotropical, Ethiopian, Oriental, and Australian biogeographic regions; *Ctenoneurus hochstetteri* (MAYR 1866), *C. myersi* KORMILEV 1953, *C. pendergrasti* KORMILEV 1971, and *C. setosus* LEE & PENDERGRAST 1977 (all endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). KORMILEV 1971 (key to genera, key to species, Oriental region, South Pacific, revision). LEE & PENDERGRAST 1977 (key to species, revision, New Zealand). MONTEITH 1997 (Australia, keyed, revision). LARIVIÈRE & LAROCHELLE 2004: 55-56 (catalogue, New Zealand).

Genus *Woodwardiessa* USINGER & MATSUDA 1959 (Fig. 42)

Synonymy (LARIVIÈRE & LAROCHELLE 2004: 56).

Description: Body subquadrate, attenuate anteriorly, pubescent (especially dorsally, on appendages, and along body margin), about 8.0-10.0 mm long. **Head**. Eyes stalked. Rostrum arising from an open atrium (open area of bucculae) not extending beyond limits of rostral groove or onto prosternum. **Thorax**. Anterolateral angles of pronotum acutely rounded, produced anteriorly. Scutellum in the form of a semicircular plate in the middle of the mesonotum, about ? as long as pronotum, without forwardly extended spines as in *Ctenoneurus*, but with distinct lobes at basal angles. Micropterous; hemelytra in the form of short pads on either side on mesonotum, not extending beyond posterior margin of abdominal tergite III (second visible). Metathoracic scent gland openings conspicuous, located just behind middle coxae, with evaporatory channel reaching to lateral margin of metapleuron. Legs with trochanters distinct (not fused to femur); femora moderately inflated, without spines. **Abdomen**. Tergal disc exposed, rather convex, rugose and pitted, with erect hairs. Dorsal abdominal scent gland openings (or scars thereof) three in number, not equally developed or spaced along the posterior margin of tergites III, IV, V (first opening large, usually strongly displaced posteriorly to middle or posterior margin of tergite IV; second rarely well developed; third obsolescent). Sternites IV, V, VI without a transverse carina along anterior margin. Other characters as for subfamily.

Included species: A single species, *Woodwardiessa quadrata* USINGER & MATSUDA 1959 (endemic to New Zealand).

References: USINGER & MATSUDA 1959 (classification, keyed, taxonomy). KOR-

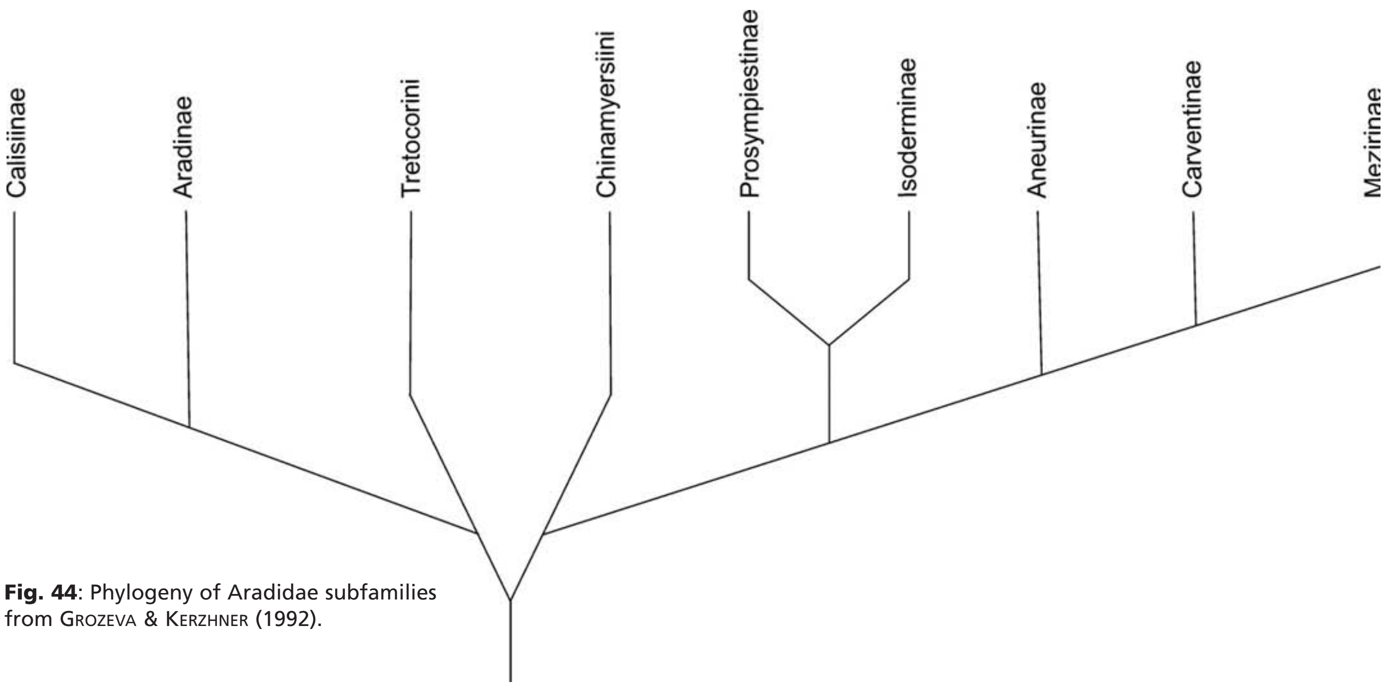

Fig. 44: Phylogeny of Aradidae subfamilies from Grozeva & Kerzhner (1992).

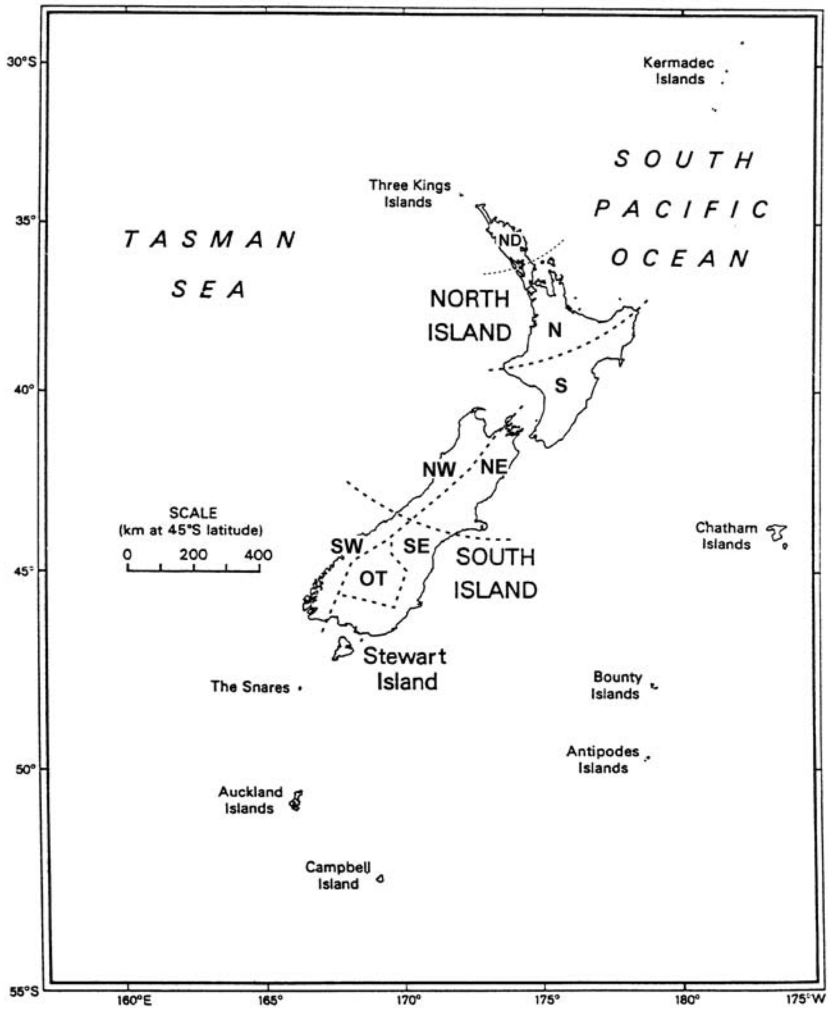

Fig. 45: The New Zealand subregion with areas of the North and South Islands: ND, Northland (northernmost North Island); N, northern North Island; S, southern North Island; NW, northwestern South Island; NE, northeastern South Island; SW, southwestern South Island; SE, southeastern South Island; OT, Otago.

Milev 1971 (keyed). Monteith 1997 (Australia, keyed, revision). Larivière & Larochelle 2004: 56-57 (catalogue, New Zealand).

Note: Kormilev (1964) described *Woodwardiessa australiensis* (= *Neophloeobia australiensis*) from Australia but transferred it as the type species of *Scirrhocoris* Kormilev 1965, which was later synonymised with *Neophloeobia* Usinger & Matsuda 1959, by Monteith (1997).

Discussion

Considerations on faunal diversification and affinities

Table 1 summarises the distribution and some of the most remarkable biological attributes of the 19 genera of New Zealand Aradidae in taxonomic sequence by subfamilies, in a manner similar to Monteith (1997) for Australian Mezirinae. The geographic regions of New Zealand used to record distributions are shown in Figure 45 and represent broadly accepted large-scale faunistic areas. Of the two main islands of New Zealand, the North Island has the most diverse fauna, with 11 out of 19 genera recorded as being endemic to it; only the genus *Neadenocoris* (Prosympiestinae) is currently known from the South Island only. Before discussing the diversification and affinities of New Zealand's aradid fauna any further, it is necessary to provide some background information into the country's natural environment.

The New Zealand environment. New Zealand lies in the south-west of the South Pacific about 1,500 km west of its nearest neighbour Australia. The country is long (c. 1600 km) and narrow, with its two main islands spanning many latitudes (c. 34°-46°S) and characterised by a complex physiography including several mountain ranges reaching great heights in the Southern Alps (South Island) and dominated by volcanic land forms on the North Island central plateau. Consequently, several climatic zones are recognised (KIRKPATRICK 1999): the northern half of the North Island has warm humid summers and mild winters (slightly cooler in the east) with an annual rainfall of 1000-2000 mm; in the central North Island (especially the central volcanic plateau) conditions vary with altitude and exposure, but many areas have a high rainfall mountain climate; the southern half of the North Island has warm summers and mild winters with high rainfall (1300-2000 mm) in the west, and very warm summers and moderate winters with lower rainfall (600-1000 mm) along the east coast; much of the eastern South Island has warm summers with cool winters (with frequent frosts and occasional snow) and annual rainfall of 500-1500 mm (slightly less inland in the extreme south); the Otago region has very hot summers, cold winters, and semiarid conditions; much of the South Island west coast has a climate that varies little throughout the year, with small temperature ranges and high rainfall increasing rapidly eastward with altitude (mountain climate conditions prevail in the Southern Alps).

In Figure 45, the North Island is divided into northern and southern regions along the "Taupo-line" – a biogeographic feature referring to a band across the central North Island at approximately 39°-39°30'S (GIBBS 1989), which roughly runs across a line of old volcanoes, with Mount Ruapehu as its focal point on the central volcanic plateau. This "line" defines more or less the current northern limit of the re-establishment of beech (*Nothofagus*) forests since the Holocene; some smaller more disjunct pockets also occur northward but usually mixed with or in close proximity to broadleaf-podocarp forests. Northland, the northernmost region of the North Island, is acknowledged as an old and geologically quite stable faunistic centre (WARDLE 1991). In addition, temperate rainforests have remained extensive there for long stretches of time, even during the last glaciation (as recently as 10,000 years ago) (WARDLE 1991) when the remainder of New Zealand was mostly covered by shrub- and grasslands with pockets of forests in the lowlands (podocarp-broadleaf in the North, beech in the South) and low-growing alpine vegetation at higher elevations.

Figure 45 also shows the South Island to be divided into eastern and western regions delimited roughly by the main divide of the Southern Alps, and into northern and southern regions at about 43°-44°S because this latitudinal range corresponds to a transitional faunistic zone observed in other insect groups (e.g., other Hemiptera and ground-beetles (Coleoptera: Carabidae)). The Otago region (including Central Otago and Otago Lakes) is a well-documented centre of biodiversity forested by *Nothofagus* until, according to MCGLONE (1988), fire permanently destroyed much of the forest about 2,500 years ago. Nowadays much of this area is covered by native grasslands (mainly tussock grasslands), open shrub- and scrublands, as well as relatively large tracts of adventive pastures.

Overall, New Zealand's vegetation cover has been altered considerably from its pre-human condition, from 75 % forest cover to only about 23 %, but WARDLE (1991) estimated that "native vegetation, albeit often greatly modified, still covers about 60 % of New Zealand; more than a quarter of it protected in national parks and other reserves."

Faunal diversification and affinities. Speculating too much on the diversification of the New Zealand fauna without more detailed taxonomic and phylogenetic analyses could be hazardous but it is possible, based on extant distribution patterns and current knowledge of the biology of New Zealand taxa, to identify some trends and formulate hypotheses for further investigation.

Tab. 1: Summary of geographic distribution and biology of the 19 genera of New Zealand Aradidae in taxonomic sequence by Subfamilies. Presence of a genus in the series of geographic regions is indicated by a solid cell (New Zealand) or X (elsewhere); black cells indicate taxa found only in northernmost North Island (Northland and/or Three Kings Islands). Entries for other columns are as follows: En=endemic (restricted) to New Zealand, Na=native, but not endemic to New Zealand; A=apterous, Mi=Micropterous, Ma=macropterous, sMa= Submacropterous, Lo=lowland, Mo=montane, Sa=Subalpine, Be=beech (Nothofagus), Br=broadleaf („evergreen"), Po=podocarp („conifer"), Sub= Subcorticolous (under tree bark), Supra=Supracorticolous (on exterior of bark of wood debris). *In *Calisius* both pairs of wings are membranous, somewhat reduced and covered by the enlarged scutellum.

						NEW ZEALAND										**AUSTRALIA**						
	Endemism	**Flight ability**	**Altitudinal range**	**Rainforest type**	**Microhabitat**	Three Kings Is	N Island (northern)	N Island (southern)	S Island (NW)	S Island (NE)	S Island (SE)	S Island (Otago)	S Island (SW)	Stewart Island	Chatham Is.	Mainland	Tasmania	Norfolk I	Lord Howe I	**NEW CALEDONIA**	**SOUTH AMERICA**	**OTHER REGIONS**
Calisiinae																						
Calisius	Na	sMa*	Lo-Sa	BrPo, Be	Supra?		▨	▨	▨	▨						X	X	X		X	X	Circumtropical
Aradinae																						
Aradus	Na	sMa-Ma	Lo-Mo	BrPo, Be	Sub		▨	▨	▨		▨	▨	▨		▨	X	X			X	X	Cosmopolitan
Chinamyersiinae																						
Tretocorini																						
Tretocoris	En	Ap	Lo-Mo	BrPo	Supra		▨	▨	▨													
Chinamyersiini																						
Chinamyersia	En	Ma	Lo-Mo	BrPo, Be	Sub		▨	▨	▨	▨	▨	▨	▨									
Prosympiestinae																						
Prosympiestini																						
Adenocoris	En	Mi	Lo-Mo	BrPo, Be	Supra?		▨	▨														
Mesadenocoris	En	Mi	Lo	BrPo	Supra		■															
Neadenocoris	En	Mi	Lo-Sa	Be	Supra				▨	▨	▨	▨	▨									
Isoderminae																						
Isodermus	Na	Ma	Lo-Sa	Be	Sub			▨	▨	▨	▨		▨	▨		X	X				Chile	
Aneurinae																						
Aneuraptera	En	Mi	Lo	BrPo	Supra		■															
Aneurus (*Aneurodellus*)	En	sMa-Ma	Lo-Sa	BrPo, Be	Sub		▨	▨	▨	▨	▨	▨	▨	▨								
Carventinae																						
Group I *Carventaptera*	En	Ap	Lo-Mo	BrPo, Be	Supra		▨	▨	▨	▨	▨											
Clavaptera	En	Ap	Lo	BrPo	Supra		■															
Leuraptera	En	Ap	Lo	BrPo	Supra		■															
Modicarventus	En	Ap	Lo	BrPo	Supra																	
Neocarventus	En	Ap	Lo-Mo	BrPo	Supra		▨	▨		▨												
Group II *Acaraptera*	Na	Ap	Lo-Mo	BrPo	Supra		▨	▨										X	X	X		Solomons
Lissaptera	Na	Ap	Lo	BrPo	Supra	■	■												X			
Mezirinae																						
Ctenoneurus	Na	Ma	Lo-Sa	BrPo, Be	Sub		▨	▨	▨	▨	▨	▨	▨			X				X		Micronesian, Melanesian, W Samoa, Ethiopian, Oriental
Woodwardiessa En	Mi	Lo	BrPo	Sub			■															

From what is known of their geographic distribution, habits, and affinities with taxa of neighbouring land masses (Table 1, see also LARIVIÈRE & LAROCHELLE 2004), there is little doubt New Zealand aradids have had a long evolutionary history closely linked to that of rainforest habitats, in particular, old Gondwanan elements such as podocarps ('conifers') and *Nothofagus* (beech) that occurred widely and were shared with other parts of Gondwana.

Aptery. Wing loss in Aradidae as an evolutionary novelty related to life in rainforest microhabitats has been discussed by MONTEITH (1969b, 1982). Submacropterous and macropterous taxa would have evolved as specialist inhabitants of the thin space (subcortical space) beneath the loose bark of dead trees in relatively open and drier forests where flight ability is required to colonise suitable habitats. On the other hand, mostly ground-dwelling, micropterous or apterous inhabitants of rainforests would have evolved a more sedentary life on the outside of bark. In such habitats, logs and other wood debris on the moist forest floor, do not shed their bark easily, usually remain to decay for long periods of time (without the subcortical space), and are in close proximity to each other. MONTEITH (1982) further elaborated that "freed from the constraints of flight ability and flat shape, and confronted with the need for camouflage, we thus see the evolution in rainforests around the world of Aradidae that have lost their wings and assumed the grotesque, tubercular form of bark-mimics. The end point of this faunal evolution appears to be a stable situation where regional aradid faunas consist of a complement of normal, macropterous, subcortical species coexisting with a complement of totally apterous, bark-exterior [supracorticolous] species."

This interpretation is supported by observations in New Zealand (Table 1) where extant taxa from putatively derived subfamilies are mostly ground-dwelling, supracorticolous, apterous or sometimes micropterous species occurring in regions that have supported rainforest habitats over long periods of geological time. In the extant New Zealand fauna, however, the full complement of wing conditions can only be observed at the family level. Suprageneric groupings show a paucity of macropterous taxa compared with continental faunas or less isolated island faunas: the Prosympiestinae are known from micropterous taxa only; the known Carventinae are all apterous; the relative ancestry of *Tretocoris* (apterous Tretocorini) and *Chinamyersia* (macropterous Chinamyersiini) cannot be established – the same situation applies to the relationship between the micropterous *Aneuraptera* and submacropterous to macropterous *Aneurus* (*Aneurodellus*) in Aneurinae; *Woodwardiessa* (micropterous Mezirinae) may be a relict Gondwanan taxon. Consequently, wing loss may have been well on its way in the ancient podocarp-dominated forests of Gondwana before New Zealand separated from it (80 mya).

Carventinae and Mezirinae. Northland, or the northernmost region of the North Island, belonged to a complex Tertiary island arc system stretching from the direction of the islands of New Guinea and New Caledonia. The Carventinae and Mezirinae of Northland are of particular interest because five monotypic micropterous or apterous genera are restricted to this region (*Mesadenocoris* – Prosympiestinae; *Aneuraptera* – Aneurinae; *Clavaptera*, *Modicarventus* – Carventinae; *Woodwardiessa* – Mezirinae). *Acaraptera* is also an interesting apterous carventine genus that was previously made up of three subgenera (*Acaraptera*, *Lissaptera* and *Nesiaptera*) until these were given full generic status by KORMILEV & FROESCHNER (1987). *Acaraptera* sensu stricto occurs on the North Island of New Zealand, Lord Howe Island, Norfolk Island (Monteith pers. comm.), the Solomon Islands, and New Caledonia, while *Nesiaptera* is found on the islands of Samoa and Fiji. *Lissaptera* is shared between the Three Kings Islands (60 km northwest of the North Island) and Lord Howe Island. *Acaraptera* sensu lato has been hypothesized by MONTEITH (1982) to represent an ancient lineage dating from the more extensive lands of the Melanesian Arc region (Eocene to late Miocene), possibly related to the genus *Biroana*, which occurs at high altitudes in the New Guinea mountains. MONTEITH (1982) also regarded *Acaraptera* sensu lato to be largely a mountain element on the islands where it occurs;

this interpretation is not supported by New Zealand data (see Table 1).

Woodwardiessa is a micropterous mezirine that may be a relict taxon with extant, more derived relatives in Australia and New Caledonia. Its morphological affinities and hypothesized phylogenetic relationship to a rainforest group of seven apterous Australian genera closely related to the New Caledonian genus *Phloeobia*, led MONTEITH (1997) to suggest an Australian plate-New Zealand-New Caledonia link maintained since before the separation of these land masses, and that the Australian and New Caledonian genera probably evolved from *Mezira*-like ancestors through forms equivalent to *Woodwardiessa*.

The world Carventinae and Mezirinae are closely related and have evolved in tropical and subtropical environments into over 60 genera and 250 species and 120 genera and 1,100 species, respectively. In these subfamilies aptery is thought to be a derived condition that has arisen many times. The absence of macropterous Carventinae from New Zealand and the extent of morphological evolution of apterous genera, mainly evidenced by thoracic and abdominal sclerite modification and fusion, together with their obvious low dispersal ability, provide support for the hypothesis that much of their evolutionary history may have occurred *in situ*, possibly in very restricted geographical areas before the breakup of New Zealand from Gondwana (80 mya) or thereafter. Further support for this idea may be offered by the low representation of Mezirinae in New Zealand and the fact that the only endemic genus is represented by the 'relict' micropterous species *Woodwardiessa quadrata*.

MONTEITH (1982) already suggested that the mostly apterous carventine faunas of Australia, New Guinea, New Zealand and New Caledonia represent an ancient element of the Southwest Pacific. In addition, the Northland region of New Zealand, where most apterous Carventinae are found, retained pockets of subtropical rainforests during much of New Zealand's geological history, which developed more recently into warm-temperate rainforests that were in existence even during the last glacial phase. As discussed above, the extant distributions of the closely related genera *Acaraptera*, *Lissaptera*, and *Nesiaptera* may provide further evidence of this Southwest Pacific link.

Chinamyersiinae. Members of this subfamily are restricted to Australia, New Zealand, New Caledonia, and Vanuatu. MONTEITH (1980) hypothesized that extant Chinamyersiinae constitute an ancient 'relict' group with two distinct lineages: the macropterous Chinamyersiini containing one species of *Gnostocoris* (Vanuatu and New Caledonia) and two species of *Chinamyersia* (New Zealand; subcorticolous); the apterous Tretocorini including three species of *Kumaressa* (eastern Australia) and one species of *Tretocoris* (New Zealand; supracorticolous). The two tribes have developed fundamental morphological differences, mainly in the stylet coiling and pretarsal pulvilli, but also differentiated body forms correlated with winged or wingless conditions and life habits. Insufficient information is available to establish with certainty the relative ancestry of these lineages. MONTEITH (1969a) thought *Kumaressa* and *Tretocoris* must have shared a common macropterous ancestor and that the sympatry of *Tretocoris* and *Chinamyersia* in New Zealand might offer some clues to that effect, but he also suggested that the morphology of the Chinamyersiini might have followed a completely different evolutionary path from that of the Tretocorini. If *Tretocoris* and *Chinamyersia* were sympatric during New Zealand's geological history, this pattern might not be so easily observed today. The authors are not suggesting that this could not be the case, but further field collecting is needed to establish whether *Chinamyersia cinerea* and *Tretocoris grandis* do in fact co-occur in the same North Island localities and habitats.

Prosympiestinae. KORMILEV & FROESCHNER (1987) recognised two tribes in this subfamily, the Llaimocorini for *Llaimocoris penai* (type species of a macropterous monotypic genus from Chile), and the Prosympiestini (New Zealand, Australia (including Tasmania), and New Guinea). Currently, *Adenocoris* (one species), *Mesadenocoris* (one species), and *Neadenocoris* (six species) are known from New Zealand, and *Prosympiestus* (four species) from eastern

Australia. Consequently, this subfamily can be regarded as having a typical eastern Gondwana distribution even though none of the extant genera and species are shared between South America, Australia and New Zealand. According to CASSIS & GROSS (2002) the Australian *Prosympiestus* species are all macropterous and most likely subcorticolous. The New Zealand Prosympiestinae, on the other hand, are all micropterous and supracorticolous. *Adenocoris* and *Mesadenocoris* occur on the North Island only. *Neadenocoris*, the most diversified and possibly more recently evolved genus, is currently known from the South Island only where species are distributed allopatrically from lowland to subalpine beech forest habitats. The cold-adapted beech forests of New Zealand did occur on Gondwana before its breakup but they are a more recent Gondwanan element than the podocarp forests. The current distribution of the three New Zealand genera and of species of *Neadenacoris* also suggests that diversification in the latter might have been facilitated by changing climatic conditions and alternate expansion and constriction of forest habitats during the Pleistocene.

Isoderminae. This subfamily includes a single genus, *Isodermus*, with a classic eastern Gondwanan distribution in Chile (one species), New Zealand (three species) and southeast Australia, including Tasmania (two species); no species is shared between these areas. *Isodermus* species are subcorticolous and macropterous in New Zealand, mostly distributed south of the 'Taupo-line' on the North Island and throughout most areas of the South Island. Their range corresponds well with the extant distribution of beech forests.

Calisiinae. This subfamily is known from six genera and about 100 species worldwide. The genus *Calisius* countains most species and occurs circumtropically. In the neighbourhood of New Zealand it is found mostly in New Guinea, Australia (southern and eastern continental, Tasmania, Norfolk Island), Melanesia (including New Caledonia) and Polynesia. Thirteen endemic species are found in Australia, with the majority in the forests of Queensland. A single endemic species, C. *zealandicus*, is found in New Zealand; although rarely collected it has been found in a number of places across the North Island and in the northern half of the South Island. Very little is known about the biology of Calisiinae in general. In the Palearctic Region *Calisius* has been observed feeding on the phloem of living trees with natural cracks in the bark (see personal communication by Kerzhner in LARIVIÈRE & LAROCHELLE 2004: 51). In Australia, species are thought to be able to fly (CASSIS & GROSS 2002). Monteith (pers. comm.) reports that they live mostly in small cracks and crevices on the outside of rough bark of dead trees and dead logs, and their dappled colour pattern gives them good camouflage in this situation – hundreds of specimens representing numerous species have been collected in this situation in Australia and New Caledonia by spraying the trunks of dead trees with pyrethrin.

In New Zealand, the habitat of C. *zealandicus* is unclear. Collecting records currently show the species to have been equally found on trees and shrubs as on fallen logs or on the ground. Records of the species coming to artificial lights (LARIVIÈRE & LAROCHELLE 2004) may provide indirect evidence of flight.

Aradinae and Aneurinae. Distributional and biological data of interest on Aradinae and Aneurinae are noted in Table 1. *Aradus australis* is the only species of Aradinae occurring in New Zealand; it is also distributed in Australia and New Caledonia. The New Zealand Aneurinae are perhaps more interesting. *Aneuraptera* and *Aneurodellus* (subgenus of *Aneurus*) are both endemic to New Zealand; the former includes a single supracorticolous micropterous species from the old pordocarp-broadleaf forests of Northland; the latter contains six subcorticolous submacropterous to macropterous species in the podocarp-broadleaf and beech forests of the North and South Islands.

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Zusammenfassung

Neunzehn Gattungen und 39 Arten der Aradidae wurden aus Neuseeland beschrieben, die meisten sind endemisch (12 Gattungen, 38 Arten). Die Arbeit gibt einen Überblick aller Gattungen und enthält erstmals einen Bestimmungsschlüssel der Unterfamilien, Triben und Gattungen. Die neuseeländischen Arten werden aufgelistet. Kurze Gattungsdiagnosen, Zeichnungen der wichtigsten Merkmale, Farbphotos aller Gattungen, ein Überblick zur wichtigsten Literatur und Angaben zur Verbreitung werden präsentiert. Die Biologie und Mannigfaltigkeit der Aradiden Neuseelands und ihre Beziehungen zu benachbarten Faunen werden diskutiert.

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