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Ko te Aitanga Pepeke o Aotearoa

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Mnesarchaeidae
(Insecta: Lepidoptera: Hepialoidea)

by

George W. Gibbs

School of Biological Sciences, Victoria University, Box 600, Wellington, 6000 New Zealand
Email: george.gibbs@vuw.ac.nz

†Niels. P. Kristensen

Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. †Deceased

**THIS VOLUME IS DEDICATED TO THE MEMORY OF NIELS PEDER KRISTENSEN
1943–2014**

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POPULAR SUMMARY

Class **Insecta**

Order **Lepidoptera**

Superfamily **Hepialoidea**

Family **Mnesarchaeidae**

From their superficial appearance, no one could possibly say that moths in the family Mnesarchaeidae deserve any special attention. They look like ordinary little brown moths and are found well away from the public gaze. Yet they rank as one of Aotearoa's natural treasures despite not even having a common name. This is due to their endemism—being entirely restricted to New Zealand, without any close relatives overseas.

Apart from a batfly, a marine caddisfly family, and four rather obscure little insect families, New Zealand insects at family level are found throughout the world. Endemism is not a visual character so the appearance of these moths is deceptive. Despite their 'ordinary' appearance, the species described here are on a par with the more familiar examples of endemic families such as our native frogs (Leiopelmatidae), kiwi (Apterygidae), kokako (Callaeatidae), rifleman (Acanthisittidae) and short-tailed bat (Mystacinidae).

As a result of this study, this moth family now contains two genera—*Mnesarchaea* and *Mnesarchella*. By 1930 seven species were known, thanks largely to the efforts of Alfred Philpott, who worked at the Cawthron Institute in Nelson. This situation persisted until the present revision was undertaken, one outcome of which has been the discovery of a cluster of seven cryptic species—i.e. species which all look deceptively similar. Now it is clear that we have at least 14 species, seven of which are described here for the first time. Unfortunately, accurate identification remains a job for the experts. ‘

Mnesarchaeids' nearest living relatives are the large Hepialidae or 'ghost moths' which include the porina and puriri moths. These two families comprise the second rung of tongued-moth evolution in the family tree of moths and butterflies—nearly as primitive as you can be if you are a moth with a tongue! The only moths below them on the tree are ericraniids in the northern hemisphere and the jaw-moths, which have to chew their food.

All mnesarchaeids are small with wingspans of 7–12 mm. They are found from October to March with a peak in December. The larvae require a lush green carpet of soft mosses and liverworts, amongst which they spin a silken tunnel system or 'lair' and eventually a cocoon for pupation. They eat almost any living plant tissue in that sward, except that of flowering plants (i.e. a diet of mosses, liverworts, fern spores, algae and fungi). The life cycle is one year with growth over autumn and winter to reach maturity in spring. Many interesting parallels between mnesarchaeid larvae and those of Hepialidae are discussed here.

No mnesarchaeid species is distributed New Zealand-wide. Each covers a discrete geographical area, some bounded by Cook Strait, others spanning the Strait as if it didn't exist. Offshore, they are known only from Hauturu (Little Barrier Island) and Aotea (Great Barrier Island).

TE WHAKARĀPOPOTOTANGA

Nā runga noa i tā te karu e kite ai, e kore rawa e taea te kī ko ngā pēpepe o te whānau Mnesarchaeidae, he pēpepe me whakanui, me kōrero ka tika. He pēpepe pakupaku, he parauri, he āhua rite ki ētahi atu momo ki te titiro atu, ka mutu kāore e kaha kitea e tūmatanui mā. Engari he puiaki tonu ēnei nō Aotearoa, ahakoa karekau ō rātou ingoa māori noa iho nei. I puiaki ai, i te mea kāore e kitea i whenua kē—kei Aotearoa anake, kāore hoki he uri tata i tāwāhi.

I tua atu i tētahi ngaro noho pekapeka, tētahi whānau caddisfly noho tai, me ētahi atu whānau pepeke iti e whā, he iti anō te mōhiotia, mō ērā atu pepeke o Aotearoa, kei ōna anō wāhi puta noa i te ao ō rātou whānau. Ehara te noho motuhake ki te whenua kotahi i te āhuatanga ka kitea e te karu, nō reira he hanga noa ēnei pēpepe ki te titiro atu. Engari ahakoa te 'māori' noa o te āhua, ko te momo e tautuhia ana i konei, e rite ana ki ērā tauira o te whānau

kāore e kitea i whenua kē e auau ana te whakahuatia, pērā i ngā poraka māori (Leiopelmatidae), te kiwi (Apterygidae), te kōkako (Callaeatidae), te titipounamu (Acanthisittidae) me te pekapeka hikupoto (Mystacinidae).

Nā tēnei rangahautanga, kua kitea e rua kē ngā puninga o te whānau pēpepe nei—kua kīia ko ngā *Mnesarchaea* me ngā *Mnesarchella*. Ka taka ki te tau 1930, e whitu ngā momo e mōhiotia ana, Me kore ake ngā mahi a Alfred Philpott, i mahi rā i te Pūtahi o Cawthron i Whakatū, i mōhiotia ai ērā momo e whitu. Kāore i rerekē ngā kōrero mō te whānau nei tae noa mai ki te mahinga o tēnei rangahau hou. Ko tētahi hua o te mahi nei, kua kitea tētahi pūreirei e whitu ōna momo, engari he tino rite te āhua ki te titiro atu. Kua mōhiotia ināianei 14 neke atu rānei ngā momo motuhake, e whitu o tērā kātahi tonu nei ka whakaahuatia, rā roto i te tuhinga nei. Heoi anō, ko te āta tautohu rawa i tēnā i tēnā momo, ka waiho mā ōna anō tohunga tērā mahi.

Ko ngā pēpepe e āhua tata ana ki ngā Mnesarchaeid, ko ngā pēpepe rahi o te kāhui Hepialidae, arā, ngā ‘pēpepe kēhua’, ko te ‘porina’ (pūrehurehu) me te pēpepe pūriri ētahi. Ko ēnei whānau nui e rua te takahanga tuarua o te kunenga mai o ngā pēpepe arero tokomanga i te rākau whakapapa o ngā pēpepe me ngā pūrerehua. Tata tonu ko te mea tawhito katoa tēnei e taea ana me he pēpepe whai arero koe! Heoi anō ngā mea kei raro iho o te rākau, ko ngā eriocraniid o te tuakoi raki me ngā pēpepe-kauwae me ngaungau rawa e rātou ā rātou kai.

Katoa ngā mnesarchaeid he pakupaku, kei te 7–12 mm te whānui mai i te pito o tētahi parihau ki tētahi. Kitea ai mai i te Whiringa-ā-nuku ki te Poutūterangi, ā, ko te Hakiheia te marama e kitea nuitia ai. Me mātua noho mai ngā torongū ki tētahi whāriki pukohu, rihawāta matomato tonu, ki reira miro haere ai i te tini ana, ā, i muri ka miroia ko te pūkoro hei moenga mō te tūngoungou. Kai ai rātou i te tino nuinga o ngā tipu ora kei te whāriki rā, hāunga anō ngā tipu whai pua (arā, he pukohu, he rihawāta, he pua atua huruwhenua, he pūkohu wai, he hekaheka āna kai). Kotahi tau te roa o te hurihanga ora. Ka tipu i te ngahuru me te takurua, hei te kōanga ka pakari. He maha ngā mea āhua rite i waenga i ngā torongū mnesarchaeid me ō ngā Hepialidae e matapakia ana i konei.

Kāore he momo mnesarchaeid kotahi nei e kitea ana i ngā tōpito katoa o Aotearoa. Ko tēnā momo kei te noho motuhake ki tōna anō rohe, ko tēnā kei tōna. Ko ētahi, ko Te Moana o Raukawa te rohenga, ko ētahi ia e kitea ana i ngā taha e rua o taua moana, me te mea nei kāore he moana i reira. I waho atu o te tuawhenua, kua kitea ētahi i Hauturu me Aotea anake.

THE CONTRIBUTORS

Niels Kristensen and George Gibbs spent much of their working lives developing their respective interests in primitive lepidoptera—NPK at the Zoological Museum, Copenhagen; GWG at Victoria University in Wellington, New Zealand. Niels was the son of an academic, politician, and ultimately the General Secretary of OECD, so it is not surprising that he was equally committed to pursuing science as well as actively participating in science administration. Our paths intersected when correspondence was initiated in 1975 by GWG seeking advice from NPK re his study of the *Mnesarchaea* head capsule (1968). Small beginnings, which in the fullness of time led to the Kristensen family spending an 8 month sabbatical in Wellington 1982–3 and GWG returning the association with a visit to Copenhagen, 1987–8. Semi-regular meetings since then around the globe have invariably had mnesarchaeids somewhere on the agenda. Niels’ wider interest has been the evolutionary morphology of primitive lepidoptera which led him to adopt all the latest tools that were being developed such as Electron Microscopy (SEM and TEM) and semi-thin histological sectioning for 3-D reconstruction of morphology. Hennig’s phylogenetic systematics gave him the methodology he needed to pursue a career unravelling the evolutionary history of hexapods, beginning with a landmark paper published in 1975, followed by five updated versions through to 1999. His standing in this field is evident from his major contribution to descriptions of hitherto unknown hexapod taxa such as a new insect order Mantophasmatodea in 2004 and a new family of Lepidoptera (Aenigmatineidae) found on Kangaroo Island, South Australia in 2015. With all these, and many more projects, publications and obligations on NPK’s agenda, including a four year directorship of the Zoological Museum, Copenhagen, and the editing of a 2-volume Handbook of Lepidoptera (1999, 2003), it is perhaps no wonder the *Mnesarchaea* project has taken so long to complete. Despite these ‘distractions’ and delays, working with NPK has been one of the most satisfying and enjoyable aspects of my career. To have a mentor who was so highly respected in his field has indeed been a very special privilege.



George Gibbs (photo by C.F. Gibbs)



Niels Kristensen (photo by T. Simonsen, see p. 10)

NGĀ KAITUHI

Mō tētahi wāhanga nui o ngā aramahi o te tokorua nei, e whai ana a Niels Kristensen rāua ko George Gibbs i ō rāua manako nui ki ngā pūrēhua tuauri, tēnā i tōna, tēnā i tōna—ko NPK i te Whare Kohinga Kararehe, i Copenhagen; ko GWG i Te Whare Wānanga o te Ūpoko o te Ika a Māui, i Pōneke, Aotearoa. He tama a Niels nā tētahi tangata kura wānanga, tōrangapū, i piki rawa ki te tūnga o te Hēkeretari Matua o te OECD. Nā whai anō pea i rite tahi ai tōna kaha ki te aru i te pūtaiao me te taha whakahaere o te ao pūtaiao. I tūhono ō māua ara i te tau 1975, i te tuhinga a GWG i tētahi kupu kimi āwhina i a NPK mō tana rangahau i te kākano pane o ngā *Mnesarchaea* (1968). He tīmatanga iti, nā wai, nā wai ka haere mai te whānau Kristensen ki Pōneke i te 1982-3 mō te 8 marama, ko te okiokinga sabbatical te kaupapa. Nō te 1987-8, ka utua tēnei e GWG i tana haere ki Copenhagen. I ōna wā anō hui ai māua, ki hea, ki hea o te ao, ko ngā mnesarchaeid tētahi o ngā mea ka kōrerohia. Ko te kaupapa whānui ake e arumia ana e Niels, ko te hanga kukunenga o ngā pūrēhua tuauri. Nā konā, ko tana hāpai ake i ngā taputapu hou o te wā, pērā i te Karu Whakarahi Irahiko (te SEM me te TEM) me ngā tapahanga mōkitokito tūārauangi hei mahi tauira ahu-3 o te hanga. Nā ngā tātaitanga whakapapa a Hennig mō te kukunetanga o te momo, ka takoto ngā tikanga hei whai māna i te roanga o tōna aramahi, ko te wewete i te kukunenga o ngā angawaho waewae ono te kaupapa. I tīmata mai i te tuhinga aronui i whakaputaina i te tau 1975; whai i muri, ko ētahi whakahoutanga e rima, tae noa ki te 1999. Tāpua kau ana tana tū i tēnei peka mātauranga, i āna koha nui ki ngā kupu whakaahua i ētahi rōpū angawaho waewae ono kīhai i mōhiotia i mua atu, pēnei i te pūtoi pēpeke hou nei, te Mantophasmatodea, i te tau 2004, me tētahi whānau Lepidoptera hou (Aenigmatineidae) i kitea i te Moutere Rūpeke, i te Tonga o Ahitereiria, i te tau 2015. I ēnei mahi katoa, tae atu ki ētahi atu kaupapa, tānga, pīkaunga kei mua i te aroaro o NPK, tae atu ki tētahi hautūtanga e whā tau te roa i te Whare Kohinga Kararehe, i Copenhagen, me te ētītanga o tētahi Pukapuka Toro mō ngā Pūrēhua, he pukapuka e 2 ōna wāhanga (1999, 2003), koia tonu pea i tino tōmuri ai te otinga o te kaupapa *Mnesarchaea*. Heoi anō, hāunga anō ēnei ‘whakawai’, ēnei whakaroaroa, ko te mahi tahi ki a NPK tētahi o ngā mea whāihua katoa, pārekareka katoa, kua mahi nei au. Nōku te hōnore nui kua noho au hei poipoinga mā tētahi tangata e pēnei rawa ana te whakamānawatia i roto i ngā kaupapa e mahi nei ia.

E tamariki tonu ana a George Gibbs (i ngā 1940) ka tīmata te whakaakona ōna ki ngā āhuatanga o te ao pepeke i Aotearoa e tana koroua, e G.V. Hudson. Engari nōna ka takahi i te ara kura wānanga i ngā 1960, kātahi anō ia ka mārama ki te wāhi nui me tōna rata nui ki te whānau pēpepe iti, mōriroriro tonu, e kīia nei ko ngāi *Mnesarchaeidae*. Kāore hoki tēnei rōpū i tino arohia e ō mua atu kaimātai pūrēhua. Ko tāna i whai ai, kia tirohia anō ngā whakapapa, me te whai kia tau he māramatanga ki ngā āhuatanga koiora o tēnā, o tēnā, mātua rā te wewete i ngā kōrero whāiti mō tō rātou oranga (Gibbs 1979), me te whakaatu i te tītaringa o ngā momo ki te mahere (Gibbs 1989). I taua takiwā, ka mārama haere te matahuhuatanga o te whānau, ka uru mai a NPK ki te kaupapa, ā, ka takoto tētahi tātai whakapapa taketake. Ināianei, i muri i te tārewatanga nui katoa pea e mōhiohia ana, kua puta tēnei pukapuka kia whitikina e ngā hihi kōpurapura o te rā, e takoto ai he kōrero poto mō ngā mea e mōhiohia ana i tēnei wā e pā ana ki ēnei pūrēhua parauri ririki o te wao nui a Tāne.

Māori translation by Hēni Jacob

ABSTRACT

The endemic New Zealand family *Mnesarchaeidae* of primitive hepialoid Lepidoptera is revised, with subdivision into two sister genera: *Mnesarchaea* Meyrick 1885 and *Mnesarchella* Gibbs, new genus and the addition of seven new species: *Mnesarchaea hudsoni* Gibbs; and *Mnesarchella dugdalei* Gibbs, *M. falcata* Gibbs, *M. ngahuru* Gibbs, *M. philpotti* Gibbs, *M. stellae* Gibbs, *M. vulcanica* Gibbs; bringing the total fauna to 14 species. *Mnesarchaeid* taxonomy remained largely unresolved for 130 years due to the look-alike maculation of seven species in the *acuta*-group. Philpott (in 1920's) recognised the value of genitalic preparations, but failed to utilise it for taxonomy, apart from resolving the status of *acuta* Philpott 1929. The present study, based on genitalic dissections of existing museum material plus extensive new field surveys, has revealed five new *acuta*-group taxa. Adults of all species are described, with colour illustrations from life and of set specimens. Diagnostic genitalic characters are given for males and females.

Although considerably smaller than hepialids, larval morphology is found to be closely similar to the known hepialoids. Pupae lack free mandibles (adecticous) but have moveable abdominal segments (semi-exarate).

Life cycle biology is reviewed. Immature stages depend on the moist 'periphyton' layer growing on banks, rocks and logs, where the larvae appear to be polyphagous feeders on fungi, algae, mosses, liverworts, fern sporangia. They spin delicate silken tunnels through which they move to feed and ultimately pupate in a light silken cocoon. Unlike those of hepialids, the eggs are remarkably large and carefully deposited, but like hepialids, possess a soft, pale yellow vitelline membrane that undergoes sclerotisation within 30 hours to become firm and black. Fecundity was determined at a maximum of 32 over a period of four days in captivity. The known phenology implies all species are univoltine with larval development throughout the winter months and the flight season in spring and summer. Diapause has not been recorded. Flight is predominantly diurnal, in dappled sunlight, but occasional specimens have been taken at UV light. Males dominate in collections, with a mean value of 15:1. Females seldom fly but wing area is reduced in only four species; their pigmentation often paler than male. *Mnesarchaeids* of both sexes display a curious 'wing-tip-lift' behaviour after alighting on a surface—the action separates and rejoins the wing tips rhythmically about twice per second.

Mnesarchaeids are distributed throughout New Zealand apart from the far north of North Island and the SE corner of South Island; they are also unknown from Stewart Island. No single species occurs throughout. Of the 14 species, 6 are endemic to North Island, 4 to South Island and 4 are found on both islands. They are unknown from offshore and outlying islands, apart from Hauturu (Little Barrier Island) and Aotea (Great Barrier Island).

Morphological features are described based on dissections, SEM and serial sectioning. Although notably smaller than Hepialidae, morphology of both adult and larval *mnesarchaeids* supports current molecular phylogenetic views. *Mnesarchaeid* autapomorphies include wing venation with a single Rs₁₊₂ vein; the lack of any positive wing-coupling mechanism; bilobed sternum A1 with external arms; male genitalia in which pseudoteguminal and valve plates are fused anteriorly to enclose a spacious subgenital crypt; female genitalia with unique elongate dorsal and subgenital plates, synscleritous anteriorly. Distinctive plesiomorphies, evident at coelolepidan level, include discrete mandibles that lack articulation or musculature; a short, coiled, functional

proboscis with intrinsic muscle fibres; a primitively 3-segmented maxillary palp; functional salivary glands (as in Lophocoronidae).

Overall the larval morphology is hepialoid but the body form differs, with thoracic segments tapering anteriorly to a more or less prognathous head position associated with a mobile life in silken tunnels. As in Hepialidae, the mouthparts are supported from a rigid oral frame with a narrow ‘lateral slit’ at the antennal socket; they also share a specialised ‘microtrichiata field’ sensory area on the prothoracic shield (incorporating D2, SD1, SD2) with certain hepialid genera. The spinneret is extremely long and mobile, associated with a silk-dependent life-style enclosed in temporary silken tunnels.

Keywords: Lepidoptera, moths, Mnesarchaeidae, taxonomy, morphology, key, New Zealand

<http://www.zoobank.org/urn:lsid:zoobank.org:pub:63642F9E-5AE6-4A73-80C5-DB68E1796E2B>

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CHECKLIST OF TAXA

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This revision represents the accumulated wisdom of a lifetime of doing what I enjoy most. How can all those who contributed along the way be adequately thanked for their help? It has taken an eternity to reach completion, during which I have lost my colleague Niels to cancer. I dedicate this volume to his memory but I cannot find suitable words to express his contribution and the times of professional satisfaction and pleasure that were such an integral part of the project. So I will simply say thank you Niels, I was the benefactor from our collaboration.

We gratefully acknowledge the stimulus and expertise so willingly given by a community of lepidopterists and other scientists to bring this account to fruition. Those assiduous field workers in New Zealand who deign to actually keep and pass on these tiny LBJ's (little brown jobs) that most entomologists ignore, and were prepared to share their collection data and enthusiasm with us over the years—John Dugdale, now enjoying his retirement from the New Zealand Arthropod Collection (NZAC); Robert Hoare who is the current curator of Lepidoptera at NZAC; Brian Patrick, John Grehan, Bill Winstanley, Ken Fox, Ian Henderson, Ian Andrew, Tom Davies, Annette Walker, Neville Hudson, Ebbe Nielsen—all have their names on those precious specimens that constitute the distribution record of Mnesarchaeidae. Thanks to you all. Then there are the morphologists and molecular biologists and others from around the world who have communicated and collaborated to add to the mnesarchaeid knowledge base—people like Yukimasa Kobayashi in Saitama with his embryological expertise; Michel Faucheux at Nantes who examined sensory organelles and Heinz Fehrenbach at Freiburg on eggshell microstructure. My visits to Copenhagen, ostensibly for work on primitive lepidoptera, have broadened my horizons thanks to the lunch-room contacts with biologists like Niels Møller Anderson, Henrik Enghoff and Jens Böcher, taking my thoughts way beyond small primitive moths with their stimulating intellectual discussions. For the retrieval of NPK's notes, papers and microscope slides of Mnesarchaeidae I am extremely grateful to Ole Karsholt and Else Kristensen, without whom this manuscript is unlikely to have surfaced again.

Robert Hoare (of NZAC) has applied his editorial skills to this presentation with inordinate patience enriched by his deep understanding of the New Zealand lepidopteran fauna and Birgit Rhode has contributed with her immaculate auto-montage images of museum specimens. We are indebted to Thomas Simonsen, Natural History Museum, Aarhus, Denmark, for his detailed and extremely helpful review of the manuscript. Brian Weigmann, Department of Entomology and Plant Pathology at North Carolina State University very generously compiled a preliminary molecular phylogenetic tree for the family that we could use in this revision. As all insect systematists know, a team of supporters is a crucial part of the entomological field work behind a project like this. In my case the loving support of my wife Keena, especially for having much of her life ruled by demands to find holiday locations at places that are not necessarily top of the 'must visit' lists. We thank The Royal Entomological Society and John Wiley & Sons, Inc. for the permission to reproduce the photo (from fig. 12; *Systematic Entomology* 40: 671–704) of Niels P. Kristensen.

PREAMBLE

This contribution was designed to fill an outstanding gap in the morphological literature on basal groups of Lepidoptera as well as provide a systematic account of the New Zealand fauna. It has had a total gestation period of 30+ years since its inception, and has been interrupted by the untimely death of Niels Peder Kristensen in December 2014. From slow beginnings on opposite sides of the world, specimens were collected, dissections and slides made, but distractions abounded. Eventually in 2014 this project was given a top priority, only to stall completely in December. Finally, thanks to the efforts of Ole Karsholt, Niels' closest colleague at ZMUC, his notes and preparations of Mnesarchaeidae that could be found were gathered together and sent to New Zealand. These items, along with notes and drawings found at his home and kindly sent by his wife Else, have enabled this resumé to be submitted for publication. Those familiar with NPK's morphological understanding and scholarly writings will immediately recognise his absence. For that I apologise but consider it better published in a form that he might not be entirely satisfied with, than not published at all. The taxonomic section is largely the work of GWG with morphological analysis contributed by NPK, as initially conceived. The depth of morphological analysis is variable, particularly with regard to musculature and internal anatomical details, coverage of which has suffered most from NPK's absence.

INTRODUCTION

Mnesarchaeidae are a small family of primitive (homoneurous) moths, which are endemic to New Zealand, and long recognized as one of the most intriguing faunal elements in this country.

The genus *Mnesarchaea* was erected in 1885 by Meyrick, who recognized its homoneurous venation and assigned it to what was then known as the family Micropterygidae [sic]. Family status was ultimately accorded to these moths by Tillyard (1919), but they continued to be considered as members of an eriocranioid assemblage. Hinton (1946) formalised this assemblage of small, diurnal moths (initially just Mnesarchaeidae and Eriocraniidae) by establishing the suborder Dacnonypha (lowermost grade of Glossata). Mnesarchaeidae finally became included in the superfamily Hepialoidea when their close affinities with were demonstrated on the basis of female genitalia (Mutuura 1972, Dugdale 1974). A high-rank taxon Exoporia was proposed by Common (1975) for the Mnesarchaeidae plus the Hepialoidea, and the monophyly of this entity has subsequently been confirmed by a number of additional mnesarchaeid/hepialid synapomorphies of adult morphology (see Kristensen 1978, 1984). Further support came with the discovery of the hepialoid-like mnesarchaeid immatures by Gibbs (1979), and subsequent studies on eggs and embryology (Fehrenbach 1989, Kobayashi & Gibbs 1991).

The two most comprehensive molecular phylogenies of lower moths available at the time of writing are from Kristensen et al. (2015) and Regier et al. (2015). The former examined 25 genetic loci from 59 lepidopteran ingroup taxa with three outgroup Trichoptera, in order to place a newly discovered family (Aenigmatineidae) into the non-ditrysian Lepidoptera tree. In their analysis, Mnesarchaeidae were confirmed as the sister group of Hepialidae (sens. lat.) and placed on the first branch of the glossatan 'Hennigian comb', along with Lophocoronidae; with Eriocraniidae on the second branch. Mnesarchaeidae and Lophocoronidae share a number of traits regarded as primitive in the Glossata, for instance their small size (comparable to that of most non-lepidopteran moths) and retention of distinct (albeit short) maxillary palps (also present in some Hepialidae), and a coilable proboscis. Regier et al.'s (2015) phylogeny of the non-ditrysian lineages reversed Eriocraniidae and Hepialoidea by placing the former on the first rung, using a larger sample of both taxa and genes. Understanding the morphology of these basal lepidopteran groups is of crucial significance for the reconstruction of a ground plan for the entire Glossata. No comprehensive morphological treatment of Mnesarchaeidae has been published to date, hence the more extended account included here than would normally be expected in an issue of Fauna of New Zealand.

The biogeographic significance of this moth family, both at local and global scale, has previously been discussed by Gibbs (1989) and is reviewed here. An analysis of mnesarchaeid nucleotides was initiated in 2000 and carried out by B.M. Weigmann. Its results are summarised in the section on Phylogeny.

FORMAL TAXONOMIC RANK

The Mnesarchaeidae and the superfamily Hepialoidea (as traditionally recognised) share a sister-group relationship with strong molecular and morphological support for monophyly. If the hepialoids are classified into one superfamily comprising five families, there is a formal justification for recognizing also a superfamily Mnesarchaeoidea (e.g., Holloway et al. 1987, Nielsen 1989). But Regier et al. (2015) synonymised Neotheoridae, Anomosetidae, Prototheoridae and Palaeosetidae with Hepialidae, rendering Hepialoidea (in the traditional sense) monotypic. They therefore considered ‘that there is little need for two superfamily names’ and that Mnesarchaeoidea should be synonymized with Hepialoidea. This makes the taxon name Exoporia redundant since the diagnostic characters for the redefined Hepialoidea are the same as for Exoporia, a recommendation followed in this revision. ‘Exoporian’ as a general descriptor remains a useful term.

BACKGROUND TO THE STUDY OF MNESARCHAEIDAE

Mnesarchaeids are neither large nor inherently attention-grabbing, and this probably accounts for the fact that only three of the early lepidopterists working in New Zealand took an interest in them and made collections to provide the basic taxonomy in use today. Coupled with that, mnesarchaeids are delicate moths and accurate species identification is far from straightforward. Francis Walker was the first to unknowingly describe a mnesarchaeid (as *Tinea fusilella*) in 1864; this species was diagnosed as a mnesarchaeid in Dugdale (1988), 124 years later, although then confused with *Mnesarchella loxoscia*. But it was Edward Meyrick, the fanatical collector of microlepidoptera, who first recognised them as distinctive and of phylogenetic significance when he was classics master at Christchurch Cathedral Grammar School during 1882–3. He found *M. paracosma* at Invercargill and Lake Wakatipu in December 1882 and returned again (from Australia) in mid-summer to collect *M. loxoscia* in the Waitakere Range, Auckland and *M. hamadelpha* on Mt Arthur, Nelson in 1885–6. All three species were recognised as Micropterygidae (sic) on the basis of their homoneurous venation, and, by 1888, were formally described by Meyrick. Considering that his sole aid to magnification was a hand-lens, his taxonomy was remarkably astute, although it included some woefully inadequate observations, such as recording ocelli present for *Mnesarchaea* when they are notably absent (Robinson 1986). Robin Tillyard, when reviewing the systematic position of Micropterygidae (sens. lat., i.e. including mnesarchaeids) raised the ranking of the genus to family Mnesarchaeidae (Tillyard 1919, p. 134).

Under the guidance of Tillyard at the newly established Cawthron Institute in Nelson, Alfred Philpott picked up the challenge of primitive Lepidoptera in 1922 and over the following five years described three more taxa, *fusca* in 1922, *similis* in 1924 and *fallax* in 1927, from the Nelson region (Philpott 1922a, 1924, 1927a); while at the same time initiating morphological studies on the group.

Philpott (1924) recognised from his studies of male genitalia that two species were confused under the name *hamadelpha*; unfortunately, he misinterpreted Meyrick’s species and therefore his new species *similis* is a synonym of *hamadelpha*. He later realised his error having consulted Meyrick and described the unnamed second species as *acuta* (Philpott 1929), accepting the synonymy of *similis* with *hamadelpha*. This synonymy had been proposed by Hudson (1928), albeit without explanation and without a full grasp of the situation (see below). NPK’s dissection of a syntype of *hamadelpha* in the BMNH in 1984 further confirmed the synonymy.

G.V. Hudson was crafting his profusely illustrated volumes on New Zealand Lepidoptera over the years that these moths were being discovered. For some reason, his contribution on mnesarchaeids was never undertaken with the same zealous enthusiasm he applied to some of his favourite lepidopteran groups. His main contribution was, as usual, the meticulous colour illustrations but, unfortunately, he also became confused over their taxonomy, with the result that only one of the four species he illustrated in 1928 (*paracosma*) was correctly named. His painting of what he called ‘*fusca*’ (pl. L fig. 2, 1928) was of its North Island look-alike (here *M. hudsoni* sp. nov.) collected from Wilton’s Bush where it was relatively common near his home. Philpott had clearly never seen or dissected specimens from the North Island, so neither of them became aware of the north-south distinction between *hudsoni* and *fusca*, as revealed by the male genitalia. With reference to fig. 24 on plate XXXIX (which shows *M. acuta*, misidentified as *M. hamadelpha*), it seems that Hudson did not accept Philpott’s recognition of two species in this group until after the 1928 publication. He correctly synonymised *similis* with *hamadelpha* (perhaps on the

advice of Meyrick), but since *hamadelpha sensu* Hudson appears to be *acuta*, he cannot have understood the full situation at this stage. This was rectified in his 1939 Supplement (with pl. LXI, Fig. 8, the true *hamadelpha*). The species he called *M. loxoscia* and painted as fig. 23 of plate XXXIX, shows the diagnostic forewing maculation of *fusilella* which, at that time, had not been recognised by any New Zealand workers and was still catalogued in BMNH under Walker's *Tinea*. Like *hudsoni*, he would have collected *fusilella* from Wilton's Bush near his home, where he collected it in good numbers. *M. loxoscia* is distinguished by a dark brown oblique patch across the base of the forewing from the eye to the mid-point of the dorsum (see Fig. 18 of the present volume). Thus, in the two volumes of *The Butterflies and Moths of New Zealand*, Hudson ultimately illustrated five of the seven species known at the time, omitting Philpott's South Island species, *M. fallax*, and *M. fusca*, neither of which he had personally collected or examined.

No additional species have been described since that time, although several of the *acuta*-group taxa described here were being collected under the mistaken assumption that they represented *acuta* Philpott. Hinton (1946) proposed a new suborder, Dacnonypha, which subsequently came to embrace a number of small homoneurous moths with a functional proboscis, including Mnesarchaeidae. This classification was accepted until Mutuura (1972) and more especially Dugdale (1974) investigated the morphology of the female reproductive system of *Mnesarchaea* as part of a comparative review of lepidopteran female genital systems, pointing out the extreme degree of reduction in the abdominal apex that made it difficult to interpret the fate of segments 9 and 10. Dugdale's use of the term 'exoporian' to describe the configuration of ovipore and copulatory pore in hepialids and mnesarchaeids was formalised by Common (1975) and widely adopted until Regier et al. (2015) rendered the name redundant as described above.

The discovery of immature stages during the 1970's confirmed the close relationship between Mnesarchaeidae and Hepialidae (Gibbs 1979). Embryological studies (Kobayashi and Gibbs 1990, 1995; Fehrenbach 1989) added further weight to the association between *Mnesarchaea* and hepialoids and the monophyly of the exoporian moths.

DIVERSITY OF MNESARCHAEIDAE

Even with the addition of the 7 new species described in this volume, bringing the overall total to 14, the family Mnesarchaeidae can scarcely be claimed diverse. They have, however, long been recognised (Gibbs 1979) as two phenetically quite distinctive species groups which are now supported by phylogenetic and morphological analyses. Here we propose to designate the divergence between the two groups with the creation of a new genus *Mnesarchella*. Initially, we had tried to avoid this distinction on the grounds that the introduction of a second genus would defeat one of the prime purposes of Linnean nomenclature—widespread recognition by way of a stable name. A case could be made for retaining *Mnesarchaea* as hitherto circumscribed, due to the taxon's importance in the context of New Zealand biogeography, whereby it has become meaningful to numerous biologists outside the circle of Lepidoptera systematists. It should be noted that Faucheux (2009), solely on the basis of differences in antennal structure, has previously suggested that both species groups should be given full generic rank. The name chosen for the new genus represents a compromise that retains the Linnean principle but establishes the fundamental divergence between these two taxa.

The two genera can be diagnosed from overall colour differences and distinctive morphological features of both sexes as follows:

***Mnesarchaea*:** a clade of four species of *dull brownish* moths with brown head and thoracic scales and the forewings indistinctly spangled with white or yellowish scales. Each flagellomere of the yellowish antennae bears a number of 3–5-branched sensilla trichodea. Male genitalia *lack the setose dorsal lobes of segment 10* (figs 59, 60); the pseudoteguminal plates, although highly variable between species, are characterised by the development of some form of conspicuous *elongate peripheral arms* associated with the membranous phallus; cornuti absent; valvae rectangular with a small bent finger-like dorsal arm separated by a deep notch, a pecten is never developed. Female genitalia with both dorsal and subgenital plates elongated and arched, nesting into one another in repose

with a common anterior articulation across the middle of the collicular region of the ductus (fig 93); *corpus bursae* a small, oval sac. Spermatheca on short duct with a single spiral turn.

Larvae green in life, unicolorous.

***Mnesarchella*:** a clade of ten species with white-scaled head and thorax; *forewings typically white or pale ochreous within the forewing cell*, bordered by a *strong brown costal streak*. Each flagellomere of the white or pale ochreous antennae bears a number of *unbranched sensilla trichodea*. Dorsum of the male genitalia with paired *rounded setose lobes on segment 10*; periphallic arms absent; ‘cornuti’ present in all but two species; darkly melanised trulleum mounds present in some species; valvae consistent throughout the group—*bilobed with a long slender dorsal arm and shovel-like ventral lobe* (figs 62–64), bearing species-specific setal features on the inner surface, often in the form of a pecten comb. Female genitalia with upper and lower genital plates as in *Mnesarchea*, but subgenital plate broad and scoop-like, hinged anteriorly with the dorsal lobe; posterior antrum of ductus largely membranous but with a melanised ‘V’-sclerite providing lateral support beneath the ovipore; *corpus bursae large, elongate* (fig 98), as long as abdomen. Spermatheca on a long duct with 2–3 spiral turns.

Larva olive-brown or greyish in life, unicolorous.

Two species groups are recognised within *Mnesarchella*; seven which share almost identical colour maculation—the *acuta*-group: where the costal streak terminates obliquely at Sc with an outwardly acute costal angle, its apex hooked inward around the end of the cell; and a monophyletic subgroup of three species the *fusilella*-group: where the costal streak terminates with an inwardly acute costal angle that lacks the inwardly hooked termination of *acuta*, or lacks the costal streak altogether.

Only six of the 14 mnesarchaeids can be confidently diagnosed from maculation alone. For the remainder (i.e. the seven *acuta*-group taxa plus *fallax*, *fusca* and *hudsoni*) genitalic dissection is recommended to confirm their identity.

METHODS AND CONVENTIONS

COLLECTION

Adult moths. From our experience, mnesarchaeids appear to be almost entirely diurnal and frequent semi-shade locations in forest or montane shrubland where they fly close to the substrate, with males hovering slowly around the vegetation, occasionally in sufficient numbers to be described as swarms, but females very seldom take flight at all. *Mnesarchella* species tend to be quite conspicuous due to their glistening white pigmentation which catches the eye. In contrast, it would be true to say that the collector is seldom aware of flight activity of *Mnesarchaea* species. Thus, as with other small moths, random sweep-netting is really the only way to reveal their presence. The true art of mnesarchaeid collection is minimising superficial damage between net and pin (see below). There are reports of male mnesarchaeid moths coming to UV light (B. Patrick, J. Dugdale, pers. comms.) (*paracosma*, *fusilella*, *loxoscia*, *dugdalei*, *hamadelpha*). Both male and female are known to stray into malaise traps on occasions (*paracosma*, *hamadelpha*).

Larvae. Larvae can readily be extracted from the rich multispecies sward of bryophytes that clothe the exposed surfaces of logs, rocks and tree-trunks in a moist forest environment. They were initially discovered during searches for the long-known larvae of Micropterigidae on their hepatic host plants. Discovery of larvae is a random process, since the actual silken tunnels constructed by mnesarchaeid larvae have never been observed in the wild. Samples of their ‘periphyton’ habitat are easily gathered and can be stored in a cool place for many days prior to Berlese funnel extraction with a low source of heat. If, instead of using preservative in the collecting vessel, the interior is kept moist with a layer of wetted plaster of Paris in the base, the extracted larvae will remain vigorously alive for a day or so; when they may be transferred to a vial of fresh substrate to observe their behaviour. With careful management of humidity, temperature and light levels to maintain condition of the substrate, plus a lot of good fortune, it is possible to induce mature larvae to construct a cocoon and pupate.

SPECIMEN PREPARATION

Although not the smallest of the Lepidoptera (see Nepticulidae, Donner & Wilkinson 1989) moths in the family Mnesarchaeidae are small enough to require special care with handling and dissection for their identification. Every effort is made here to provide the most direct means for determining species identity but it needs to be stressed that with a series of cryptic species, whose proper identity has eluded previous generations of lepidopterists, accurate determination in the field is not usually possible. Specimen preparation which renders the male genitalia structures visible, is essential for discriminating between certain *Mnesarchella* species but in some cases wing maculation is sufficient, provided the specimen is in near-perfect condition. To ensure this for pinned specimens, or photographs, the live insects must be kept cool (e.g. refrigerator) beforehand. To minimise scale loss it is recommended that vials containing freshly-caught insects be transferred from net to a cool storage place by way of a vacuum flask, charged with blocks of ice.

For this study, pinning and spreading of the wings was achieved by briefly anaesthetising the insect in ethyl acetate vapour until all movement ceases (not more than one minute) and then inserting a micro-pin that has been wetted with a strong solution of nicotine. The muscles remain relaxed, enabling the wings to be spread and pinned for museum specimens before muscle contraction sets in and the insect becomes rigid. These dried specimens are suitable for genitalia preparation as described below. Alternatively, killing in the fumes of ammonia avoids the nicotine step and leaves specimens beautifully relaxed. To avoid damage from condensation in the killing jar, keep the moths in their vials and replace the lid with a nylon mesh cloth attached by a rubber band.

For DNA extraction fresh specimens are best put directly into 95% ethanol; for detailed morphological study (histology) fixation is required, as described, e.g. by Nielsen and Kristensen (1989).

It is anticipated that samples for identification will often be less than perfect. They may be in alcohol, or virtually lacking wing-scales if from a malaise trap for example. If preserved in alcohol, all that may be required is to lightly brush all scales off the posterior tip of the abdomen. A series of diagrams is provided (Figs 65–78) with the express purpose of illustrating the appearance of the male genitalia without dissection (i.e. with parts in situ). If the specimen is dry, or the above preparation is insufficient to show diagnostic characters, the abdomen will need to be removed and macerated in 10% KOH in an aqueous solution to clear soft tissue and extend the cuticular parts needed for identification. With pinned specimens, this can be achieved by gently lifting the abdomen to break the joint with the thorax; wetting in 70% alcohol and placing in 10% KOH. Warming to just below boiling point for about 5 minutes should be sufficient to permit scale removal and to see the basic structures. After KOH treatment the abdomen is washed in alcohol and a temporary slide mount made by placing it, ventral side uppermost, in a drop of glycerine. Magnification of 80–100x will reveal the diagnostic features given in the key. (*Mnesarchaea* specimens should be viewed dorsally, *Mnesarchella* ventrally) Note that the appearance of the membranous phallus region and associated cornuti varies greatly in different specimen preparations. The diagrams show it extended with the cornuti clearly displayed. On many specimens the cornuti will appear more "internal", i.e. overlaid by heavily melanised structures and hence less clearly visible.

For permanent mounts (Euparal is recommended for this) the convention is to "open" the male genitalia along the hinge line of the subgenital crypt as shown in the taxonomic drawings (e.g. Figs 79–92). This displays the inner surfaces of the trulleum and valvae simultaneously and can be done with the aid of a pair of mounted minuten pins prior to placing the cover glass in position. With *fallax* this technique is more difficult due to the bulbous nature of the genital capsule in that species. Female genitalia should be mounted ventral side uppermost. Light staining with 1% Chlorazol Black E in 70% alcohol is recommended before making permanent mounts.

PHOTOGRAPHY

With the improvements that have taken place to macrophotography over recent years, it is now a very practical option to grab high quality photographic images at the time specimens are being collected and prepared for taxonomy. These images can reveal details that would otherwise escape attention when examining standard taxonomic collections. The images used here were taken with a Pentax 100D digital reflex camera, using a 100mm macro lens on a 100mm extension tube. Lighting was from two Sunpak B3000 flash units mounted 20 cm apart on a sheet aluminium base to which the camera is attached. To retain the sometimes hyperactive individual moths, the

photos were taken inside a fine mesh cage hanging from a 600mm diameter ring suspended about 700mm above a bench or table top. By encouraging the moth to perch on a moveable leaf, the image could be orientated at will. Droplets of water directed from a hand spray onto the leaf surface are useful to distract moths and interrupt their movements.

CONVENTIONS

Each species treated here has been recognized on the basis of its distinctive morphological features. In all cases these species circumscriptions have been compatible with the known molecular, biogeographic and ecological data. The family, as we interpret it, comprises 14 discrete species, some of which are confusingly similar on their external characters. However, as pointed out by Philpott (1927b), their genitalic characters are remarkably diverse. Over 900 specimens have been examined in this study with genitalic preparations made for 190. They are notable for the consistency of the characters used.

The species concept applied here is thus the Morphological Species Concept (MSC) in which a species is recognised by its discrete morphology. Were it necessary, molecular phylogenetic analysis would have been accepted as the arbitrator of taxonomic decisions where it gives relationships based on monophyly and shared derived characters. In practice the morphological species are supported by phylogeny. Thus it can be stated that our species concept is a combination of both MSC and PSC (Phylogenetic Species Concept).

REPOSITORIES

AMNZ—Auckland Institute and War Memorial Museum, Auckland, New Zealand.

BMNH—Natural History Museum, London, England.

BPNZ—B. H. Patrick private collection, Christchurch, New Zealand.

CMNZ—Canterbury Museum, Christchurch, New Zealand.

GGNZ—Author's private collection, Eastbourne, New Zealand

IHNZ—I.M. Henderson private collection, Massey University, Palmerston North

LUNZ—Dept. of Entomology, Lincoln University, New Zealand.

MONZ—Te Papa Museum of New Zealand, Wellington, New Zealand.

NZAC—New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand.

ZMUC—Zoological Museum, University of Copenhagen, Denmark

Two letter codes used to define the New Zealand locality districts follow Crosby et al. (1998).

AUTHORSHIP

In this joint publication, NPK was responsible for the morphological analysis and interpretation resulting from serial histology that was used for building up a comparative view of this family taxon and how it relates to other basal homoneuran moths. 'On location' at his home base, GWG was able to collect the fauna, provide suitably fixed specimens for sectioning, and prepare the basic taxonomy. NPK has been on the fringe of molecular biology as it came to dominance but, like GWG, has remained outside its practitioners. We agreed that a resumé of this family should necessarily include a molecular analysis and are most grateful that Brian Weigmann kindly undertook to fulfil that role.

MORPHOLOGY OF RELEVANCE FOR IDENTIFICATION

These brief notes are intended to provide a guide for identification purposes, i.e. to interpret structural details used in the keys and descriptions. A detailed comparative morphological account of the family follows the systematic section of this contribution.

ADULT MOTHS

Wing maculation is clearly important, hence the emphasis on colour illustrations here (Figs 1–18, 136–156). Visual recognition of a mnesarchaeid moth can be achieved for 6 of the species from colour patterns alone (*paracosma*, *fallax*, *dugdalei*, *loxoscia*, *fusilella*, *philpotti*). The remainder, as Philpott (1927b) pointed out, require male genitalia for confirmation. Since these structures are of a unique type within the Lepidoptera, rendering conventional lepidopteran understanding and terminology of little value, a brief outline of genital morphology and the terms used for its description is fundamental to successful identification. Size measurements and superficial features of the head and antennae or wing venation contribute little of value for diagnosing species.

The basic structure of mnesarchaeid genitalia of both sexes is best understood as a voluminous pouch that opens dorso-ventrally by way of a transverse hinge across the anterior end. The pouch functions as a terminal clasp; in the male for seizing and holding the apex of the female abdomen during copulation; and in the female for holding and orientating the huge ovum. Here the terminology of the male genital capsule is derived from Hepialidae; particularly from the Australian genus *Fraus* as described by Nielsen and Kristensen (1989). (See Figs 58–60, 62, 79–83 for terminology). The focus is a spacious **subgenital crypt**. Its roof is formed from a pair of dorsal **pseudoteguminal plates**, offering a number of sclerotised components which are taxonomically useful – including a variety of **long periphallic arms** (Figs 79–82) in *Mnesarchaea* or a darkly melanised **trulleum saddle** in *Mnesarchella* (Fig. 83). Dorsally, the abdomen of *Mnesarchella* species terminates in a pair of simple setose **dorsum 10 lobes**, between which is the median membranous anal ‘cone’ (Fig. 83). These A10 lobes are uninformative for systematics of *Mnesarchella* species and are absent from *Mnesarchaea* species, apart from *fallax* (Fig. 79). Below the anal opening is a complexly folded membranous region marking the aperture to the **phallocrypt** (Figs 41, 58). In the absence of discrete phallic sclerotisations (a feature of nearly all Hepialoidea) the most visible phallic component in macerated specimens is usually a voluminous inflated membrane. In addition, a small cluster of needle-like **cornuti** may be evident (Fig. 83), but have a limited value in taxonomy. Ventrally, the floor of the subgenital crypt is formed from a pair of prominent shovel-like **valvae** and their anterior arms. In *Mnesarchella* the inner valva surface is characterised by an area of strong medially-directed bristles, often organised into a comb-like **pecten** (e.g., Figs 83–85). Significantly, the subgenital crypt of all species features a pair of blunt knob-like ‘hinges’ at its anterolateral extremities, formed from the fusion of anterior arms of the pseudoteguminal plates dorsally with the arms of the valvae ventrally (a mnesarchaeid apomorphy). These synscleritous ‘hinges’ allow the cavity to gape widely posteriorly, thereby accommodating the bulky female terminalia. Features of taxonomic value are best revealed when the subgenital crypt is ‘opened’ at the hinge—the rationale behind genitalic slide mount preparations (Figs 79–92). Also obvious in these preparations is the median ventral **vinculum**, a sclerotisation of segment 9, always well developed (Fig. 79). The juxta, often a prominent feature of hepialids, is not evident in Mnesarchaeidae.

Female genitalia of mnesarchaeids (Figs 93–108) illustrate an extreme reduction of the abdominal apex, whereby the 8th tergite, or **dorsal plate**, and the ventral sternite, or **subgenital plate**, are opposable, enclosing a voluminous genital pouch (**antrum**), with the anus and ovipore on the ceiling and the entrance to the corpus bursae (ostium) at the anterior end on the floor (Figs 93, 98, 99). This **exoporian condition** was clearly documented by Dugdale (1974). In *Mnesarchella* the subgenital plate is broad, roughly as long as wide and the margins of the antrum are marked by melanised lateral bands which extend forward to fuse near the entrance to the bursa, forming what we refer to as the ‘**V**’-sclerite (Fig. 99). Fine details of the female morphology are taxonomically informative but to nowhere near the extent of male genitalia. In *Mnesarchaea* both dorsal and subgenital plates are elongated, 1.7 to 2.5 x longer than wide, slightly arched in lateral view and nesting into one another (Figs 94–97). The ‘**V**’-sclerite is absent.

LIFE HISTORY AND BIOLOGY

Adult behaviour and oviposition. Our understanding of adult behaviour is the result of opportunistic rather than directed study. It is presented here in the hope that it will stimulate further interest. In captivity, freshly emerged

females survive for about 4–5 days. They imbibe water from wet leaf surfaces (see Fig. 19) but have never been observed visiting flowers in the wild. Their natural lifespan is unknown.

Males fly frequently, preferring shade or filtered sunshine and can be active in humid misty weather. Their flights are close to the ground where they tend to hover around vegetation. With the predominantly white species such as *Mnesarchella fusilella* it is possible to locate females by visually searching the periphyton or its associated fern fronds and seedlings around areas where males are seen to be assembling. Females seldom fly, although their wing area is equivalent to that of the male in all but *paracosma*, *philpotti*, *ngahuru* and *hamadelpha* where female wing area is reduced to 80–90% that of the male. The ratio of males:females in collections has a mean value of about 15:1 with a range from 3:1 in *dugdalei* and *loxoscia* to 36:1 in *ngahuru*. A malaise flight intercept trap on a ridge-top location in the Tararua Range provided 24 males:4 females of *hamadelpha* over several days, implying a distinctly lower flight frequency of females compared with males. A sweepnet, used so that it gently scrapes the surface of the periphyton mat, is the best way to seek females. Courtship behaviour has not been observed but several mating pairs of *fusilella* have been found resting on periphyton, implying that mating occurs directly after emergence of the female. Copulation has a minimum duration of 30 minutes and occurs late morning in that species. The moths face in opposite directions with their wingtips meshed together, male on the outside. The antennae of both individuals are laid back almost touching the dorsum, in contrast to their normally erect position. Courtship of this type is considered indicative of sex pheromone emission from females but to date no evidence has been found of how that might be achieved and no comprehensive behaviour experiments have been completed. Abdominal sternum 5 glands are absent in this family.

Both sexes of mnesarchaeids exhibit a curious little wing movement when settling from a flight or after a short run along the substrate. A stationary moth normally holds its wings steeply tentwise over the abdomen (see colour figures). The movement referred to involves a rapid lifting of the wing tips out from the body, a slight separation, and then return to the resting position; the action being rhythmically repeated three or four times (sometimes more) at the rate of one or two per second. Similar behaviour is characteristic of *Glyphipterix* spp., Glyphipterigidae (R.J.B. Hoare, pers. comm.). These are also diurnal and with a ‘distracting’ wing apex pattern.

Oviposition begins on the day of copulation. The large pale yellow oval eggs are deposited singly, placed on, or wedged between, the leaves of foliaceous liverworts and mosses. Adhesion, if it occurs at all, seems to be simply due to the wet surfaces of the leaves; there is no evidence of a sticky substance. Fecundity of wild females held in suitable containers for oviposition has reached a maximum of 32 in *acuta* (Gibbs 1979), 27 in *fusilella*, over a four-day period. This is extremely low for a hepialoid moth where numbers in the thousands are commonplace, but the eggs are large (0.48 x 0.32mm), each representing a major metabolic investment for a moth of this size. Egg shells of hepialoid moths feature an outer thin, brittle chorion and a thick rigid vitelline envelope (Fehrenbach 1995). The newly laid eggs of mnesarchaeids and hepialids exhibit a unique hardening of the vitelline membrane, which is the result of a process of sclerotisation. It is initiated by the oocyte at the time of egg deposition, causing the pale yellow fertile eggs to turn black after about 30 hours (Fig. 23) (Kobayashi & Gibbs 1989). The same phenomenon has been reported in the case of *Ogygioses* Issiki & Stringer 1932 (Regier et al. 2015). The mnesarchaeid egg shell splits longitudinally at eclosion and is not eaten by the larva.

Larva. Mnesarchaeid larvae have a lifestyle which, apart from their diminutive size (maximum length 9mm), is very reminiscent of others in their sister-group, the Hepialidae. It is based on their use of silk-lined tunnels within the encrusting mat of periphyton (a term for a multi-species complex of bryophytes and hepatics which smothers rotting logs, old tree stumps, rocks and soil surfaces in damp forested areas) (Gibbs 1979). The larva constructs a multilayered sheet and tunnel system within the green and decaying foliage where it lives and moves. The tunnels link areas of sheet-web, the whole forming a three-dimensional system of silk runways (Figs 20, 21). The larva rests within a major tunnel, able to retreat rapidly along it, forwards or backwards, if disturbed. Presumably the larva obtains its food directly from the runways but actual browsing has not been observed. It thus spends its entire life "walking on silk". Their rapid movement within the tunnels appears to be aided by the non-hooked proleg crochets (Figs 132, 133). Off the silk, on a smooth surface, their locomotion lacks control, they move forward more slowly, and tend to resort to a "semi-looper" style in which the first and second pairs of prolegs are lifted from the substrate. Adaptation to silk-lined tunnels is thus reflected in their overall shape, in particular their labial and proleg morphology.

Fresh faecal pellet analysis shows that a wide range of food material is ingested by the larvae, including moss leaves, liverwort leaves and rhizoids, fern sporangia, fungal spores and hyphae, and filamentous algae. No comparative feeding studies have been made between mnesarchaeid species but it is interesting to note that the polyphagous mnesarchaeid diet appears broadly similar to the Hepialidae (*sens. lat.*), where it can oscillate between mycophagy (= saprophagy) in early instars to phytophagy in later stages of *Aenetus* (Grehan 1989; Dugdale 1994). Two of the minor exoporian families incorporated into Hepialidae—Anomoseidae and Palaeoseidae—have been partially reared (Regier et al. 2015), sufficient to reveal a number of parallels with mnesarchaeids. In Australia *Anomoses* (formerly Anomoseidae) has been reared from a ‘rotten log’, implying that it might be mycophagous; and in Taiwan, *Ogygoses* (formerly Palaeoseidae) has been obtained from a mossy substrate where the larvae make mnesarchaeid-type silken tunnels. They are also reported as having a prognathous head with the clypeus protruding over the labrum. At this stage the limited knowledge of mnesarchaeid diets offers no evidence of angiosperm tissue being consumed by either larvae or adults. Clearly there is much to be learned about the structural and behavioural characteristics of basal hepialoid larvae. All mnesarchaeid larvae found to date have been extracted from moist periphyton samples with the aid of Berlese-type funnels. They have not occurred in leaf litter samples nor in periphyton that can be easily desiccated e.g. in exposed sunny sites or on twigs or tree trunks above the ground. On the other hand, species composition of the periphyton appears to be relatively unimportant (but that could be simply a matter of ignorance).

Pupation. At maturity the larva spins a cocoon and contracts to about half its former length. The cocoon is oval (5.5 x 2.2mm in *acuta*, Fig. 22) camouflaged with fragments of debris on the outside, lined with smooth white silk. It is possible that the wild pupal site could be within the soil since the only known cocoon (of *loxoscia*), picked up in the field by J.S. Dugdale (pers. com.), beneath hepatics was covered with clay particles.

In contrast to the larval stages, which share a lifestyle and morphology closely similar to hepialids, the mnesarchaeid pupa exhibits features that are more reminiscent of small endoporian Lepidoptera. Their protective cocoon eliminates the need to wriggle along a substantial tunnel before emergence and this, combined with their small size (3–4mm), might explain their departure from what has come to be understood as the ‘normal type’ of exoporian pupa (Dugdale 1994; Nielsen & Kristensen 1989). Prior to emergence of the adult moth, the pharate adult is able to open the cocoon by means of a terminal “cocoon cutter” on the vertex of the head, and project itself through the hole, aided by a pair of lateral spines and a series of rear-facing dorsal spines (Figs 117, 118). As in many cocooned endoporian pupae, the last pair of dorsal spines (on A8) are reversed and function to anchor the exuviae in the cocoon while the emerging adult struggles to free itself.

Pathogens and parasites. All that can be said is that this is a fertile field for investigation. Dead larvae have not been examined for pathogens and no parasitoids have been reported from the rearing attempts of any species of mnesarchaeid.

PHENOLOGY

Phenology. Adults are active throughout the warmer months from October to April. Each species has a fairly well-defined flight period as shown in Fig. 134. December is clearly ‘mnesarchaeid month’ with all but one of the species having been collected in this month and nine species with a December peak. Although the data on which this Table are based have been accumulated from nearly 300 locality records, it needs to be appreciated that they were not collected in a strictly scientific manner. Extended records from single localities are not available for most species but where they are, they show flight periods which range from as short as 3 weeks (for *fusilella* at Otari Native Plant Reserve WN), through 7 weeks (for *acuta* at 5-mile track, Rimutaka Range WN) to 8 weeks (for *paracosma* in a Dunedin garden DN). Note that these data are cumulative over successive years so that in any one year the flight period is likely to be shorter than indicated here. The records indicate well synchronised life cycles, a conclusion supported by samples of larvae.

Seasonal flight periods range from an early spring species, *fusilella*, with its peak in late October, to the autumnal *hudsoni* which peaks in March. The sister species, *fusilella* and *loxoscia*, are normally separated by geographic location and by a difference in their peak flight activity of about five weeks. However, they are known

to co-occur on the Waitakere Range AK, the Mamaku Plateau BP, and the Herangi Range WO and at the latter locality J.S. Dugdale has obtained both species on the same day (10 December).

Eggs hatch in about 3–4 weeks and larvae grow through autumn, winter and early spring to reach mature size in August–September. The exception is *hudsoni* with a significant growth phase in mid-summer, reaching maturity by the end of January. Lowland species, and possibly all mnesarchaeids, are univoltine, developing without diapause so far as is known. A possible instance of two-year development is discussed on p 41. Pupation occurs about one month prior to the emergence of the adult.

PHYLOGENY

The hepialoid family Mnesarchaeidae ranks among the most noteworthy components of the New Zealand fauna. Not only is it endemic, but it occupies a key position as sister group to the diverse, world-wide Hepialidae (in the sense of Regier et al. 2015). Mnesarchaeids are arguably the most generalised of all glossatan moth groups except for their genitalia. They are small, homoneurous, tongued but with vestigial mandibles that lack any trace of musculature – all features shared with the Australian Lophocoronidae. Both the morphological evidence presented here and current molecular understanding support the monophyly of Mnesarchaeidae + Hepialidae. For this part of the world, the position of Lophocoronidae is of particular interest but, until larvae can be found, this question will have to remain on hold. The Regier et al. (2015) tree places lophocoronids as sister to Hepialoidea (Hepialidae + Mnesarchaeidae), a position that conflicts with the earlier morphological interpretation of Nielsen and Kristensen (1996), in which they were sister group to the remainder of Glossata (including Exoporia). Clearly, significant gaps await attention before any further resolution of the relationships of basal Glossata is possible.

The only molecular resolution of mnesarchaeid phylogeny to date has been that of Brian Wiegmann, carried out in 2001 (unpublished). We acknowledge that it did not constitute a focus of this study and remains as a weak part, not being up to the standard expected today. Three portions of the mitochondrial genome (16S, COI and II and ND1) were sequenced for 17 mnesarchaeid specimens. Two eastern Australian Hepialidae, *Elhamma australasiae* Walker, 1856 and *Oxyeanus dirempta* (Walker, 1865) were used as outgroups. Parsimony analysis of the combined data under ACCTRAN optimization in the program PAUP*4.5b7 yielded two equally parsimonious trees from 231 parsimony informative sites: the trees differ only in the relative placement of *fallax* and *paracosma* in one clade. The phylogeny is presented in its most basic form as Fig. 135 to provide a framework for discussing the relationships and biogeography of Mnesarchaeidae. The 14 species of Mnesarchaeidae revealed in this analysis formed two strongly supported clusters, here defined as the genera *Mnesarchaea* (four species) and *Mnesarchella* (ten species). The analysis also convincingly groups *dugdalei*, *fusilella* and *loxoscia* as a discrete monophyletic clade. Four pairs of sister species are identified in the analysis and discussed below in relation to biogeography.

BIOGEOGRAPHY

The islands of New Zealand are well known for their high level of endemism. The list of endemic animals includes 15 family-level taxa, 6 of which are invertebrates (Gibbs 2016). It is accepted that the most likely explanation for these is that they represent surviving relics of formerly more widespread groups. With some endemic families there is fossil evidence available in support of this view (e.g. with short-tailed bat family Mystacinidae where fossils are known from Australia; or the frog family Leiopelmatidae, with fossils from Patagonian Argentina), but in the case of Mnesarchaeidae, the absence of fossils is a situation which is unlikely to change anytime soon. New Zealand's neighbours—Australia, New Guinea or New Caledonia—would appear to be the most probable locations to discover further mnesarchaeids or related taxa, but to date, mnesarchaeids remain endemic to New Zealand despite intensive searches offshore.

In the absence of any attempt at molecular dating using comprehensive taxon sampling, we must resort to what can be gleaned from existing lepidopteran phylogenies. Fortunately, Wahlberg et al. (2013) have provided a molecular fossil-calibrated age estimate for the divergence of basal lepidopteran lineages. Their phylogeny implies

that the Jurassic was an important period for the early diversification of non-ditrysian lineages, and the Cretaceous was the time when all major ditrysian lineages diverged from each other. Their estimates are older than previously hypothesised. The date for the divergence of exoporian taxa is shown as mid-Cretaceous, about 120 Ma, with Mnesarchaeidae diverging from Hepialidae around 90 Ma. These estimates imply that tectonics and vicariance explanations might well account for the diversity of extant exoporian lineages i.e. Mnesarchaeidae and the hepialid lineages formerly treated as families, on the lands surrounding the SW Pacific (Australia and New Zealand), a theme taken up and discussed by Grehan and Mielke (2018). They speculate that the current overlap of hepialids and mnesarchaeids in New Zealand can be explained as the result of tectonic isolation of the region when East Gondwana expanded into the Pacific following retreat of the Pacific Plate subduction zone. In their scenario, subduction left the widespread ancestral 'Exoporia' with a marginal pre-mnesarchaeid isolate, separate from the more widely distributed pre-hepialid ancestor. Grehan and Mielke suggest that the belt of magmatic activity known in New Zealand as the Median Batholith may have been associated with this separation. It is envisaged that subsequent range expansion by Hepialidae resulted in the current overlap of these two groups in New Zealand today. The closely related, non-exoporian Lophocoronidae (Regier et al. 2015; Kristensen et al. 2015), distributed across Australia today, is likely to share parts of this interpretation. At the time of writing, the best that can be said is that molecules (Wahlberg et al. 2013) and Gondwanan tectonics are providing a plausible Mid-Late Cretaceous hypothesis to account for the presence of Mnesarchaeidae as an endemic New Zealand group. The conclusion is that the isolation of Mnesarchaeidae probably occurred prior to (possibly long before) the opening of the Tasman Sea, which did not begin until 80 Ma. In the light of these evolutionary scenarios, the biogeographic juxtaposition of Mnesarchaeidae with their diverse exoporian relatives in the SW Pacific is scarcely surprising.

Within New Zealand, the geographic record of 14 mnesarchaeid species shown on the accompanying maps has reached the point where an attempt to ascribe patterns to underlying geological features is relevant. First, it is notable that hardly any mnesarchaeid has been found beyond the two main islands of New Zealand, not even on Stewart Island. To date, Hauturu (Little Barrier Island, *Mnesarchaea hudsoni*) and Aotea (Great Barrier Island, *Mnesarchella loxoscia*) are the only offshore islands where mnesarchaeids occur, a situation that will possibly be amended with more intensive faunal sampling.

The only previous attempt to review the distribution of Mnesarchaeidae within New Zealand in relation to possible geological drivers (Gibbs 1989), suggested that a significant feature of this family was the high species diversity on the central North Island volcanic plateau, higher than in NW Nelson which has long been regarded as a major centre for New Zealand species diversity. This disjunct pattern appeared to be reinforced by the presence of four disjunct species-pairs that occur between central North Island and NW Nelson, thus highlighting a significant distribution gap across the southern North Island. Further collecting since 1989 has extended two of these volcanic plateau distributions further south, into the southern North Island, thereby to some extent reducing the significance of this pattern. At the time of writing, with the availability of the molecular study reviewed above and updated distribution maps, we can offer a revised viewpoint on their distribution patterns.

The first point from the molecular analysis is the strong support it gives to the subdivision of Mnesarchaeidae into *Mnesarchaea* and *Mnesarchella*. Although no estimate of dating is available, it suggests these two clades might be considered independently for biogeographic analyses. Within the *Mnesarchaea* clade, distribution of the putative stem species *fallax* seems independent of the existence of Cook Strait. In contrast, *fusca* and *hudsoni* comprise a strongly supported sister-pair, borne out by molecules, morphology and distribution data; each widely distributed yet allopatric about Cook Strait, a water barrier claimed to be no older than a mid-Pleistocene Interglacial period at about 1 mya (Lewis et al. 1994). Intriguingly, the crown group trio of *Mnesarchella dugdalei* / *fusilella* / *loxoscia* make up a widely-distributed, yet broadly sympatric clade throughout the North Island. These three species show an overall weak seasonal isolation; *fusilella* and *dugdalei* flying in spring (Oct–Nov), *loxoscia* in mid-summer (Dec–Jan), but their seasonal separation is far from absolute as recent collectors have found. This situation implies a history of mobilism/dispersal but gives no leads for the proposal of geological hypotheses relevant to their modern distribution limits. These forest species are very dependent on fluctuations in forest cover that have taken place during ice advances of the Pleistocene (McGlone 1985) and hence their modern distributions do not necessarily reflect earlier evolutionary events.

It is the disjunct sister-species pairs that hold the key to some possible geological drivers of mnesarchaeid evolution. Apart from the trio of species above, the genus *Mnesarchella* contains two sister-pair groupings—

vulcanica / *acuta* and *falcata* / *stellae*. In both cases, the more northern member of the distribution (*vulcanica* or *falcata*), is focussed around the North Island volcanic plateau, while the southern member (*acuta* or *stellae*) is centred in NW Nelson. The southern sector of this pattern suggests there might be a deeper causal event behind the vicariance—namely the Alpine Fault, which marks the boundary between Australian and Pacific Plates, initiated 23 mya and with a lateral displacement of 470 km since then. These two species are confined to the west of the fault in the South Island but exhibit very different biogeographic patterns. *M. acuta* is currently the most widely distributed and abundant of all mnesarchaeid species, whereas *stellae* appears to show a relict distribution, restricted solely to a few locations in the neighbouring Karamea-Mokihinui catchments. *Mnesarchella acuta* and *Mnesarchaea paracosma* are the only widely distributed South Island mnesarchaeids, with the former largely west of the Alpine Fault while the latter occupies the landscapes east of it. A plausible hypothesis might be that following isolation by early Alpine fault movement, *acuta* has had an opportunity for dynamic range expansion, possibly in quite recent times (i.e. within the last 1 Ma) when Cook Strait was profoundly changing the geography of central New Zealand; allowing *acuta* to colonise the lower North Island as far as the Manawatu Gorge and extend into Canterbury as post-glacial forest recovery provided suitable habitats to the east and in the south as far as Fox Glacier.

For an overall picture, we can suggest possible roles for both post-Oligocene sea level fluctuations during the archipelagic phase of our landscape history and the patchiness of suitable forest habitats during Quaternary cooling as ice ages came and went, but without even a preliminary dating hypothesis of mnesarchaeid divergences we are not prepared to speculate further on the drivers of the current distribution patterns.

What is surprising from more extensive recent field collecting, is that mnesarchaeids are seemingly absent from the far north of North Island, i.e. Te Pahi, Maungataniwha Range and Puketi Forest; as well as from the far south, i.e. the Catlins, Longwood Range and including Stewart Island. A phylogeographic approach at molecular level, coupled with more intensive collecting, has the potential to shed further light on the evolutionary geography of this family.

ADULT MORPHOLOGY

Previous morphological work on adult mnesarchaeids has been largely confined to integumental structure: head/mouthparts (Tillyard 1923, Kristensen 1968), venation/wing coupling/wing scales (Tillyard 1923; Philpott 1922a, 1922b; Kristensen 1970, Simonsen 2001), male and female genital segments (Philpott 1927b; Mutuura 1972; Dugdale 1974). Preliminary observations on some phylogenetically informative traits in mnesarchaeid 'soft' anatomy are reported in a comparative context in Nielsen and Kristensen (1996). Available information on mnesarchaeid immatures includes data on eggshell ultrastructure (Fehrenbach 1989), early embryogenesis (Kobayashi & Gibbs 1990, 1995), and outlines of larval and pupal external structure (Gibbs 1979; see also Grehan 1981, Nielsen & Kristensen 1989).

Our present account of mnesarchaeid morphology has two principal objectives. Firstly we want to disclose the overall diversity exhibited by recent mnesarchaeids and to use the findings for species discrimination and classification. Secondly we want to make inferences about the mnesarchaeid ground plan, with the purpose of using these inferences (a) to assist the reconstruction of the ground plan of the Hepialoidea, and (b) to assist the determination of character-state polarities within the Hepialoidea for future phylogenetic analyses of this superfamily. The coverage of our morphological observations was intended to largely follow the standards set in detailed accounts of the Lophocoronidae (Nielsen & Kristensen 1996) and of the hepialoid genus *Fraus* (Nielsen & Kristensen 1989). However, with the loss of NPK's contribution, this treatment has necessarily been abbreviated. The terminology of Lepidoptera morphology is approaching stability; comprehensive accounts are given by Kristensen (1998) and Hasenfuss & Kristensen (2003).

HEAD CAPSULE (Figs 26, 27, 28, 29, 36, 37, 54, 55). Our use of the terms dorsal/ventral and anterior/posterior refer to an orientation of the head in which the plane of the occipital foramen is normal to the insect's long axis. (Thus, fig. 1 of Kristensen 1968 purports to illustrate the head of *M. loxoscia* in 'anterior view', but with the orientation adopted here (and indeed in the following fig. 2 as well), the projection is more anterodorsal/dorsal.) Head proportions in different taxa should, of course, be compared from comparable viewing angles.

Neolepidopteran moth heads, with their scarcity of external 'landmarks', may require particular attention in this respect.

As in other hepialoids the head is virtually devoid of sutures (sulci). A weak transverse thickening between the ventral rims of the antennal sockets (Kristensen 1968: 'interantennal sulcus') is sometimes discernible, and there may be a similar thickening between the dorsal rims as well. The presence of such thickenings may lead to the illusive impression, that the area between the antennal sockets is in itself particularly weakly sclerotized (Kristensen 1968, for *M. loxoscia*: 'weakly sclerotized line'), which is not the case. A postoccipital suture is always represented by thickenings along the occipital foramen, ventrally (i.e., between the occipital condyles and the upper border of the postlabial sclerotization) and dorsally; the latter thickening is continued a short distance laterad as a 'temporal' suture.

A blunt lobe is produced from the dorsal rim of the antennal socket, opposite the commonplace ventral condyle but extending more mediad. This lobe, the 'dorsal antennal condyle', is particularly prominent in some *Mnesarchella* species. There is no indication on any of the examined species of Mnesarchaeidae of sensillum-bearing processes on the vertex.

Ocelli are lacking, as in all hepialoids. Compound eyes with close-packed facets, devoid of setae; the facets densely sculptured with micro-nipples (7 per micron). The supraocular index is high by neolepidopteran standards—about 0.4; the interocular index is about 0.7. In the absence of mandibular muscles (see Nielsen & Kristensen 1996) these figures are indicative of a relatively weak development of the compound eyes: the greatest diameter of the latter is about half (0.45 in male *Mnesarchaea fusca*, 0.52 in male *M. paracosma*, 0.47 in male *Mnesarchella fusilella*) of the mesonotum length (Figs 26, 54).

The posterior head surface is almost plane to slightly concave. The occipital condyles are long and slender, their upper margins are on level with, or even below, the upper wall of the corporotentorium. The condyle apices are bent backward and almost meet in the midline immediately above the posteromedian tentorial process; they are united by thick mesocuticle to the apices of the laterocervicalia.

Tentorium. The anterior tentorial pits are situated about midway between the mandible and the outer corner of the antennal sockets, while the posterior pits are situated basally in the occipital condyles. The anterior tentorial arms fuse with the corporotentorium so close to the posterior pits that one cannot talk of the existence of posterior tentorial arms. The distance between the posterior pits is so much smaller than that between the anterior pits, that the anterior arms converge strongly posteriorly. In lateral view the anterior arms are approximately straight (with only a slight dorsally convex curvature). Strongly developed dorsal arms arise from the anterior arms about one-third from the anterior pits; these arms are almost straight, and their apices are not attached to the head capsule. There are no ventral processes on the anterior arms. The posteromedian process on the corporotentorium is strong, but slender.

Vestiture. The upper and anterior head surfaces have a dense vestiture of narrow scales (Fig. 27). The clypeal area below the anterior tentorial pits is scale-free, as is most of the posterior head surface. The narrow zone between the antennal bases and compound eyes may or may not be scaled. A single row of rigid, ribbed setae (Fig. 28), encircle the compound eyes, largely concealed beneath the dense scale vestiture of the head. These have not been recorded on other hepialoid groups or Lophocoronidae and could possibly be an autapomorphy for Mnesarchaeidae.

ANTENNAE (Figs 30–33). Mnesarchaeid antennae are 0.5–0.7x forewing length in male (0.4–0.5 in female). The scape and pedicel are of commonplace structure. The flagellum is filiform, consisting of 31–43 segments ('flagellomeres') in the male (28–37 in female). A higher number (>36) is probably plesiomorphic, and occurs only in *fallax*, the three *fusilella* subgroup species and *philpotti*.

Vestiture. The flagellomeres have a characteristic surface texture of wavy ridges forming an elaborate network (Fig. 30), which becomes increasingly densely packed on the more distal flagellomeres. Microtrichia are absent on the more basal flagellomeres (except in *fallax*), appear sparsely from about half way along the antenna and become moderately dense on the terminal flagellomeres. All flagellomeres are largely covered by narrow, apically notched scales, the sockets of which are particularly concentrated in a proximal zone of each flagellomere (Figs 31, 33). In *Mnesarchaea* species they are restricted to this zone, while in *Mnesarchella* a few may occur, more scatteredly, on the distal part also. A total of 12 types of sensilla have been identified, including different

types of multiporous sensilla basiconica and sensilla styloconica (Faucheux & Gibbs 2008). Of particular note are the 2–6 branched multiporous sensilla basiconica which are a feature of the *Mnesarchaea* species and a strong autapomorphic character for this genus. The unbranched multiporous sensilla auricillica (cf. Simonsen 2018: fig. 114), basiconica and trichodea are likewise a feature of *Mnesarchella*.

Musculature. The extrinsic antennal muscles arise on the anterior part of the tentorium, including the dorsal arms.

Remarks. The long filiform mnesarchaeid antennae without densely microtrichiated flagellomeres are unique plesiomorphies in the Hepialoidea. Insufficient studies are available for wide-ranging comparative comments among the hepialoid families but suffice to say the sensilla reported here are also present on Lophocoronidae. The ascoids of micropterigid antennae are more ‘formalised’ and fixed in position than the multiporous sensilla of mnesarchaeids but probably serve a similar function. Faucheux and Gibbs (2008) suggest the multiporous sensilla of mnesarchaeid antennae are very likely to be receptors of the hypothesised sex pheromones which appear to drive the random, hovering type of flight behaviour in males (see p. 17–18).

MOUTHPARTS (Figs 26, 29, 34–37, 54, 55). The labrum is much reduced, but while practically indistinguishable in ordinarily mounted cleared preparations, it can be recognized, as a small, flat flap by SEM observation (Fig. 26) and in sagittal sections. Its lateral corners do not bear seta bundles comparable to those of eulepidopteran ‘pilifers’ (Krenn & Kristensen 2000).

Mandibles are relatively large, medially flattened lobes (Figs 26, 29, 36, 54); their smooth cuticle is indented slightly on the outer aspect in *acuta*, with a few irregular microtrichia. A campaniform sensilla is present adjacent to the cranium. Mandibular musculature is absent.

The complete absence of mandibular muscles is unsurprising in adult neolepidopterans, because the adecticous pupal type precludes a function for the pharate adult’s mandibles. Still, a reduced muscle complement is reported from scattered higher moths, and a vestigial tentorio-mandibular muscle has also been recorded from the generalised hepialoid *Fraus* (Nielsen & Kristensen 1989).

Maxillae (Fig. 55) have the basal piece (morphologically probably a cardo+basistipes, see Kristensen & Nielsen 1979: 118) articulating with the lower cranial margin just mediad from the anterolateral corner of the postlabial sclerite. The distal margin of this basal piece is somewhat thickened and sharply bent (following the general bend between the posterior and ventral head surfaces); there are no strengthening ridges across the sclerite. The dististipes has the proximal apex bent, and its medial margin bears an internal ridge.

The maxillary palp is short, ranging from about one-quarter head width in *fusca* to one-fifth in *acuta*. There are three distinct palp segments in all species examined. The mid-segment apparently corresponds to segment 2+3 in the five-segmented palp of the glossatan (and lepidopteran) ground plan; as indicated by the bend between the basal and mid-segment, as well as by the fact that the latter may bear, at least dorsally, a membranous groove that indicates the site of the former segmental boundary. The basal segment is naked, the mid and distal segments sparsely scaled (Fig. 26).

The galeal proboscis is well developed and functional in all mnesarchaeids; its length varies between 1.2 and 1.4 times the head width, and when tightly spiralled in repose it forms two to three coils.

Labium-hypopharynx: The postlabium is an arched, convex sclerite, densely covered with elongate (piliform and narrowly lamellar) scales (Fig. 37). In contrast, the apically bilobed prelabium (‘prementum’) is naked; its proximal margin is strengthened by an internal crest, and it is separated from the postlabium by a membranous area.

(**Note:** Kristensen (1968) described—and illustrated (fig. 2)—the mnesarchaeid ‘prementum’ as ‘narrow’. However, the impression that this sclerite is particularly narrow—in the anterior/posterior direction; ‘short’ would, therefore, have been a more appropriate term—is largely due to the fact that its proximal, flat area lies on the topographically lower surface of the head and therefore is greatly foreshortened, if at all discernible, in whole-mount preparations where the head rests on its posterior surface.)

The ligula-hypopharynx lobe is short, blunt and thin-walled, its ventrolateral walls mesocuticular.

The **labial palp** is also three-segmented, but is more than twice the length of the maxillary palp. All segments are densely scaled, though the basal one is naked proximally (Figs 26, 27, 55). An invaginated cluster of sensilla, known as vom Rath’s organ, is present on the terminal segment, subapical in all species except *fallax* where it is

terminal (Figs 34, 35). It consists of a small circular depression containing a tight cluster of elongate sensilla with projecting apices.

The **sitophore** (see Nielsen & Kristensen 1996 for a terminology discussion) is an elongate, triangular sclerite, which is broad at its anterior base immediately above the salivary orifice; it tapers gradually, as it smoothly curves backwards along the upper surface of the suboesophageal ganglion.

The two **salivary glands** are united into a common duct a short distance behind the salivarium, and they terminate near the prothoracic-mesothoracic boundary; as generally in glossatan Lepidoptera they are simple tubes.

Remarks. Long-standing confusion has existed over the question of the specialised lepidopteran vom Rath's organ in Mnesarchaeidae. The uncertainty arose following Kristensen's (1968) claim that the organ had been lost in Mnesarchaeidae. The labial palps of mnesarchaeids have now been investigated by Faucheux (2010), who clearly showed that the sensory pit is present in the five species he examined. All 14 species of the family have been examined in the present study to reach our conclusion.

Salivary glands have not been reported from other adult Hepialoidea but, not surprisingly, are present in Lophocoronidae, where the galea are also functional.

THORAX (Figs 46, 47, 56, 57). Our investigation of the thoracic region remains incomplete apart from the following comments made by NPK before his death.

Prothorax. The laterocervicalia are almost U-shaped, with long and slender anterior and posteromedian arms; the former are devoid of proprioceptive setae. The posterolateral corner of each laterocervicale articulates with the pleural front margin clearly above the 'anepisternal tooth', which is a very prominent process from the anterior pleural margin.

The foretibia bears an epiphysis, well developed in eight of the species but with variable expression, approaching vestigial or absent, in the others (Fig. 48).

Pterothoracic notum. The anterior margin of the metanotum is clearly a little convex; however, the proportions of the pterothoracic segments remain rather primitive, with the meta-alinotum in the mid-line being about 0.54–55x that of the meso-alinotum.

Remarks. While the meta-/meso(alinotum) ratio in mnesarchaeids is lower than in the Lophocoronidae (ca 0.64) it is higher than in some Neopseustidae (0.47 in *Synempora*) and among the highest in the Neolepidoptera.

Wings. (Figs 56, 57) The wings of Mnesarchaeidae are the smallest of all Hepialoidea (3.5 mm fwl) and possess the most reduced venation; characters that are presumably linked. Their shape is rather more pointed apically than in other hepialoids, with a forewing length/width ratio of 0.26–0.28.

Forewing. The humeral vein is absent. The subcosta remains unbranched with the exception of a few aberrant individuals of *Mnesarchella* where a small terminal fork can be evident.

The swollen common base of the radial vein on the forewing is characterised by a dense patch of campaniform sensilla (Fig. 51). The R vein is unbranched in all Hepialoidea, but it is a unique feature of all Mnesarchaeidae that **Rs1+2 is represented by a single vein** only (Figs 56, 57). The stem of the radial sector is short to very short. Rs3 and Rs4 are stalked in mnesarchaeids, with Rs3 terminating on the costa and Rs4 on the termen. The fork of Rs3+4 is very characteristically symmetrical about the apex. (Simonsen and Kristensen (2017) listed 'Rs3 reaching wing margin posterior to apex' as an autapomorphy of Hepialidae in the sense of Regier et al. (2015): termination of Rs3 on the costa in Mnesarchaeidae supports this inference.)

M1 is stalked with the stem of Rs3+4 in 8 species of *Mnesarchella*, a unique situation within the Hepialoidea (Fig. 57), but the two veins arise separately in *fusilella*, *loxoscia* and the four *Mnesarchaea* species (Fig. 56). The inter-M crossvein is normally absent but a weak M-CuA crossvein is present.

CuA is forked but CuP is weak, not reaching to the margin. There is a single, simple anal vein.

Hindwing. The above characters also apply to the hindwing, with the exception of the M-Cu crossvein, which is absent. In the hindwing of all species, M1 is not stalked with Rs3+4, thus resembling the situation in the forewing

of *Mnesarchaea* where the two veins arise separately. In 8 species (*hudsoni*, *acuta*, *falcata*, *hamadelpha*, *stellae*, *vulcanica*, *dugdalei*, *fusilella*) Rs1+2 arises from the stem of Rs3+4 a short distance beyond the cell.

Vestiture. An investigation of wing scale morphology by Simonsen (2001) reviews their condition in *Mnesarchella hamadelpha* and *Mnesarchaea hudsoni*. Briefly, mnesarchaeid dorsal wing scales are arranged in two layers, with outer hollow scales overlying inner fused (=solid) scales. A difference between the ground scales of *hudsoni* (short rounded scales) and *hamadelpha* (short and somewhat dentate scales) was detected by Simonsen (2001, figs 8G, 8B). The hollow scales (Figs 50, 53) have the Neolepidoptera pattern of ridges (primary and secondary), cross-ribs and perforations. Perforations are vestigial on the ground scales (Fig. 52).

Coupling mechanism. Tillyard (1919) drew attention to the reduced jugal lobe in *Mnesarchaea*, and Philpott (1922b) pointed out that the jugal lobe in *Mnesarchaea* seemed ‘inadequate as a coupling-apparatus.’ Moreover, a cluster of about 20 stiff hairs (bases do not differ from those of normal wing scales) which might function like frenular bristles in higher lepidopterans, were also ‘weak and unsatisfactory’. He concluded that wing-coupling was achieved by the interlocking of a long band of piliform scales along the lower side of forewing dorsum with a similar row on the hindwing costa. We doubt that either of these proposed mechanisms could function to couple the wings and propose that mnesarchaeids in flight, like *Eriocrania* and hepialids (Mallet 1984; Grodnitsky & Kozlov 1985) beat the two pairs of wings independently. Thus the fringing scales (Fig. 49) are not a wing-coupling device at all.

Remarks. The absence of the humeral vein is unique within the Lophocoronidae + Hepialoidea clade, and must be considered a diagnostic autapomorphy of the Mnesarchaeidae within this group. The stalking of M1 with Rs3+4 in the forewing of some species is obviously an apomorphic character. The same type of stalking occurs in both wings of the Acanthopteroctetidae (Davis 1978), and it is recurrent in several heteroneuran lineages, particularly in narrow-winged forms.

THORACO-ABDOMINAL BOUNDARY REGION (Figs 46, 47). The meta-laterophragmata are of very modest size. Sclerotisation of the first abdominal segment, apart from sternum 1, closely resembles the condition described for *Fraus* (Nielsen & Kristensen 1989) with the dorsum sclerotised only along the anterior and lateral margins (Fig. 47). The strongly sclerotised lateral margin (‘tergal brace’) extends from the ‘lateral intersegmental pouch’ (‘sinus’ of Dugdale 1994) to the anterolateral corner of tergum 2, bifurcating at about its mid-length to form a ventral articulation point with the tergo-sternal brace. This brace, a conspicuous darkly sclerotised rod, curves inwards to connect the tergal brace to the apex of a long anterior extension of the dorsal margin of sternum 2, a configuration which delineates a rear-opening pouch in the lateral body wall behind spiracle 1.

Venter 1 is membranous apart from a distinct sternum 1 sclerite which has a most distinctive shape. Its two posterior corners are extended as delicate spreading arms which project freely from the body wall (Figs 46, 47). The form of sternum 1 is consistent in all Mnesarchaeidae and constitutes an important synapomorphy for the family.

Segment 2 bears a simple more-or-less rectangular tergite and sternite with strengthened lateral margins. Sternum 2 is represented by two distinct sclerites as in many monotrysian families (Davis 1986), a small anterior portion (2a) which is darkly melanised but varies in shape from rectangular or oval to crescent-shaped in different species, and a broad sternum 2, poorly defined except along its dorsal margin.

MALE POSTABDOMEN AND GENITALIA (Figs 38–43, 58–92). **Integument.** There is no trace of the sternum A5 glandular structures found in six other primitive lepidopteran families (Djernaes & Sperling 2011; Kristensen et al. 2015). The hindmost unmodified abdominal segment is A7; A8 is shorter than the preceding segments.

The basic structure of the genital segments shows important similarities to that of other Hepialoidea, and the terminology here applied is based on Nielsen and Kristensen (1989) and Dugdale (1994). As in most insects, the complex characters of the male genital region are of very considerable taxonomic significance in the family, as already shown in the preliminary work by Philpott (1927b).

A ventral sclerotization of segment A9, the **vinculum**, is always well developed; in *Mnesarchella* it is consistently crescent-shaped, the anterior margin smoothly convex, whereas two of the *Mnesarchaea* species (*fallax*, *paracosma*) have the anterior margin markedly concave (Figs 79, 82). As in other Hepialoidea, a sizable anterior portion of the vinculum is apodemal.

The dorsum of A9 does not bear a discrete sclerotization. In *Mnesarchella* the abdominal dorsum terminates in a pair of unmelanised rounded lobes, densely clothed with microtrichia and setae (Fig. 41). These lobes, which were attributed to the 'tegumen', i.e., the dorsum of A9, by Philpott (1927b), are here ascribed to segment A10; they are very similar to, and undoubtedly homologous with, the paired **dorsum A10 lobes** which are of widespread occurrence in primitive Lepidoptera and apparently pertain to the ground plan of the order (Kristensen 1984, 2003). In *Mnesarchaea*, segment A10 bears comparable dorsal lobes only in *fallax* itself, where they have a very lateral position. The ventral/inner surface of each *fallax* lobe bears a conspicuously melanised concave sclerite adorned with strong spines.

Segment A11, i.e. the '**anal cone**', is a small and simple, median membranous bulge surrounding the anal opening which may have a terminal, or (particularly in some *Mnesarchella* species) a markedly dorsal position.

All Hepialoidea have topographically dorsal, mostly paired sclerotizations above/laterad from the genito-anal field. These sclerotizations (usually termed 'tegumen' by earlier authors) are now attributed to the lateroventral areas of A10 and are referred to as the '**pseudoteguminal plates**' (Nielsen & Kristensen 1989) (see Figs 58–60 for terminology). The plates in question are variably developed in the Mnesarchaeidae. Contrary to conditions in many Hepialidae their lateral parts are not set off as paired discrete 'intermediate plates' (such plates were found by Simonsen & Kristensen (2017) to be a synapomorphy for *Fraus*, *Afrotheora*, *Antihepialus* and Hepialidae *sensu stricto*). In *Mnesarchaea* species, the plates are contiguous or synscleritous in the mid-line between the anus and the genital field, and they uniquely bear a variety of prominent long '**periphallic arms**' which enclose the entrance of the phallocrypt (see below) between them (Figs 65–68). The outer surface of each arm is sclerotized while the inner surface is membranous and in *hudsoni*, the arm bases are separated from the rest of the pseudoteguminal plates by narrow strips of mesocuticle. In all Mnesarchaeidae, the lateral parts of the pseudoteguminal plates are synscleritous with the inner valve bases (see below), produced as distinct arms around the anterior face of the subgenital crypt cavity (Fig. 39). The periphallic arms of *Mnesarchaea* are highly characteristic of each of the species. These periphallic arms constitute a pair of '**subanal arms**' issuing from the base of the anal cone, although in the asymmetrical *paracosma* there is only a single arm, which is near-medial and markedly curved; and supports the anal cone for a considerable length. *M. hudsoni* and *paracosma* have additional pairs of '**lateral arms**' arising from the pseudoteguminal plates. These processes appear to be positional homologues of the lateral spinose plates on the ventral/inner surface of the dorsum 10 lobes of *fallax*, which are synscleritous with the pseudoteguminal plate.

(**Note.** Nielsen and Kristensen (1989) and Simonsen (2018) used the term 'pseudoteguminal arms' for the homologue in *Fraus* (Hepialoidea) of the processes here called periphallic arms. The presence in some Mnesarchaeidae of as many as three pairs of posterior processes from the pseudoteguminal plates necessitates a more differentiated terminology.)

In *Mnesarchella* species, ventral extensions of the pseudoteguminal plates support the genital field from below; these sclerotizations may be separated medially, or they may form a complete bridge; in six species they bear prominent, very darkly melanised, ruggedly textured mounds (e.g. Fig. 43). This texture is strongly reminiscent of that on the '**trulleum**' of some hepialoids, and according to the positional criterion these sclerotizations are indeed homologous. In *Mnesarchaea* species there is no 'trulleum' sclerotisation as such, but some distance in front of the bases of the periphallic arms the two pseudoteguminal plates are united ventrally by a more or less distinctly melanised bridge which apparently is a trulleum homologue.

In *Mnesarchaea fallax*, a pair of branched tubes with dense epithelial cells and a conspicuously thickened (procuticular) intima apparently open close to the midline just in front of the bases of the periphallic arms; the non-enlarged epithelium and the intima thickness is unexpected for glandular formations, but we feel unable to suggest an alternative function for the tubes. Most *Mnesarchella* species have in a corresponding location, i.e., just behind the trulleum mounds/bridge, a sharply delimited oval membranous area in which an opening is identifiable with SEM examination or in histological sections (Figs 38, 39, 58, 84, 85, 87, 90–92: gl). The opening leads into a

cavity, the strongly folded walls of which are lined with thin cuticle. The function of these formations remains unknown; there is no histological evidence of the epithelium being secretory.

The **valvae** (gonopods) are always bilobed, with the dorsal lobe forming a slender arm. In *Mnesarchella* the entire dorsal valve margin is straight or smoothly curved; the shovel-like ventral lobe bears numerous strong setae on the inner surface, in eight species the latter are concentrated into a comb-like patch or row (pecten) of extra heavy, blunt melanised setae (e.g., Fig. 84). In *Mnesarchaea* species the valvae are roughly rectangular, and the small finger-like dorsal arm is sharply bent downward. Piliiform scales on the outer surface grade into thin setae towards the upper arm, and there may be a patch of setae on the inner face, but never a distinct pecten. All mnesarchaeids have the proximal lateral arms of the valva more or less prominently produced anteriorly, where their median apices are fused to the pseudoteguminal plates. In *fallax* it has been noted that the exposed distal end of the valve can be folded into the subgenital crypt space in repose (as in Fig. 38).

The space above the bases of the valvae is referred to as the **subgenital crypt**. The roof of the subgenital crypt is formed by the pseudoteguminal plates and its derivatives, and/or the unsclerotized body wall below (topographically in front of) the latter. In *Mnesarchaea*, two very different configurations of the crypt floor occur: *fallax* is unique in the family in having a mid-ventral sclerotization, which posteriorly is separated by narrow membranous zones from the valvae, while anterolaterally it is synscleritous with the latter. Anteriorly this median sclerotization is joined to the anterior margin of the pseudoteguminal plate by a narrow strip of mesocuticle, while the lateral parts of the 'bottom' of the subgenital crypt (at the valve/pseudoteguminal plate transitions) bear fully sclerotized cuticle; arguably the mid-ventral sclerotization is homologous with the juxta in hepialids and can be thus named. In the *fusca* subgroup a 'juxta' is represented only by a ribbon-like sclerite in the shape of an (anteriorly open) U, the arms of which lie adjacent to the inner valve bases; the epidermis of the soft body wall between the arms of the U is markedly thickened and in all probability secretory. In *Mnesarchella* species, the valvae are always separated by an unspecialized mid-ventral membranous region.

As in other Hepialoidea there is no sclerotized phallus tube. In *Mnesarchaea* the phallocrypt can be a very long tubular invagination (e.g. in *M. hudsoni*, extending to near the A4–A5 boundary); as noted above, the crypt opening is flanked by the periphallic arms arising from the pseudoteguminal plates. In the examined members of *Mnesarchella*, an evaginable phallus has not been observed and no periphallic arms are developed except in *falcata*, where a pair of diagnostic subanal arms is evident (Figs 40, 70, 84). In 8 of the *Mnesarchella* species (exceptions *fusilella*, *philpotti*) the cuticular intima of the male duct bears posteriorly a pair of variably developed 'cornuti'/cornutus groups, which may indeed be homologous with similarly termed formations in Acanthopteroctetidae and many Heteroneura; no counterparts of these structures occur in *Mnesarchaea*.

Musculature. The intrinsic musculature of the male genital segments has now been studied in exemplars of a large proportion of the lepidopteran families (Kuznetsov & Stekolnikov 2001; see also Hasenfuss & Kristensen 2003). In the case of mnesarchaeids this musculature was investigated by NPK for the present study, based on examination of serial sections of *fallax*, *fusca*, *hudsoni*, *paracosma*, *acuta*, *falcata*, *loxoscia* and *fusilella*. He found that hepialoid male genitalia muscles are difficult to homologise with entities in the generalised lepidopteran muscle complement, and unexpectedly the difficulties with those of the mnesarchaeids proved even greater. Without NPK's final input, this task has become beyond the scope of this publication.

Remarks. Although detailed musculature is omitted from this study, it seems appropriate to draw attention to a notable set of transverse muscles which are variably expressed within the family in relation to the long pseudoteguminal arms. Originating on the lateral areas of the pseudoteguminal plates, they run above and below the rectum, above the phallocrypt. They are very powerful in *Mnesarchaea* species and strongly developed in *Mnesarchella falcata* (Fig. 40), yet almost unidentifiable in *M. fusilella*, implying they are associated with actions of the pseudoteguminal arms. These muscles are homologous to the G8 muscles illustrated by Dugdale (1994, figs 144–147) for New Zealand hepialids. It would be interesting to examine the role of these highly variable arms during male sexual activity. Homologous sclerotised arms are present in males of some *Fraus* species and in *Prototheora*.

Internal genitalia. The two testes are located near the A4–A5 boundary; they are contiguous in the midline and surrounded by a common fat body envelope. Their follicle walls are very delicate and the arrangement of the follicles is difficult to make out; from favourably placed sections through the follicle bases it does appear that there

are four of them per testis as would be expected. The wide efferent ducts immediately adjacent to the testes have a tall-celled epithelium with large nuclei. Eventually the duct diameter diminishes and the nuclei account for less of the cell volumes. The duct is then widened into a spacious seminal vesicle.

Some of the examined male specimens of *Mnesarchella* have secretion masses protruding from the phallus; in one *M. loxoscia* the mass is as long as 1.1 mm. These masses consist of granular material similar to that occurring in the duct, but no spermatozoa were detected in these cases. It cannot be ascertained whether the protrusion of these masses is a natural phenomenon or an artifact triggered by fixation.

FEMALE GENITALIA (Figs 44, 45, 93–108). **Integument.** The exoporian condition of the female genitalia of Mnesarchaeidae was suggested by Mutuura (1972) and well demonstrated by Dugdale (1974). The functional design of mnesarchaeid genitalia is complex. The cuticle-bearing parts of the two genera are distinctive, but within each group there are cases where species-level differentiation, if at all recognizable, is limited to minor details of spinosity and the like.

The hindmost unmodified abdominal segment is A7. The apex of the abdomen carries a dorsal and a ventral sclerite that we here denote the **dorsal genital plate**, presumably formed through fusion of terga A8+9+10, and the **subgenital plate** respectively (corresponding to the antevaginal lamella in Hepialidae (e.g. Simonsen 2015, 2018, Simonsen & Kristensen 2017)). The dorsal plate tapers posteriorly and is more or less deeply indented in the midline; the posterolateral lobes thereby produced differ markedly between the two genera. Sclerotization of the dorsal plate is weak except for the lateral margins. The subgenital plate is slightly shorter than the dorsal plate, and as in the latter, its shape is characteristic of each genus. In *Mnesarchaea*, the subgenital plate is broader than the dorsal plate anteriorly. Its lateral margins overlap those of the latter and separate into independent lateral arms before joining with the ventral plate at the point of fusion (Figs 93–97). In *Mnesarchella* the ventral plate remains slightly narrower than the dorsal plate (Figs 98–108). All mnesarchaeids have the dorsal and subgenital plates fused anterolaterally, the *Mnesarchella* species at a single point—the *Mnesarchaea* species over a considerable distance. In the latter genus the anterolateral parts of the subgenital plate may be more or less pronouncedly bent outwards/backwards, thereby forming a pair of pockets behind sternum 7.

The anus and ovipore are located in the membranous body wall below the hind margin of the dorsal plate (Fig. 98); between the two openings is an ill-defined median subanal plate which we have not found to be taxonomically useful.

The posterior margin of the subgenital plate is the lower lip of the copulatory orifice and its sclerotization is continued into that of the posteriormost part of the floor of the genital chamber. This sclerotization extends forwards as a pair of lateral bands, which in most *Mnesarchella* species are somewhat elevated and strongly melanized, eventually converging to fuse in the midline near the anterior end of the antrum, forming the distinctive '**V-sclerite**'. In *Mnesarchaea* species the bands bear high ridges which are eventually united by sclerotized cuticle, but the melanization of these sclerotizations is less intense than in *Mnesarchella*, so that in cleared whole mount preparations they are generally much less evident. The dorsal and ventral walls of the genital chamber have diverse surface textures and adornments that can play a role in taxonomic distinctions (Figs 44, 45). In all species, the longitudinal sclerotised bands/ridges on the genital chamber floor appear to fit into matching grooves in the roof. Although the complex cross-sectional outline of the genital chamber, particularly in *Mnesarchaea* species, renders its structure very difficult to interpret from whole mount preparations, it suggests that these grooves probably function as sperm tracts.

Internal genitalia. We use the term **antrum** to denote the entire part of the genital chamber which contains sclerotizations. Anteriorly the antrum leads into the **bursa copulatrix** proper, which is divisible into the narrow posterior **ductus bursae** and the widened anterior **corpus bursae**. The spinosity of the ductus intima and the size/shape of the corpus are taxonomically informative at various levels.

The cuticular intima of the **spermatheca** is observable in well cleaned whole mount preparations, preferably after staining. It is the proximal two-compartment portion of the **ductus spermathecae**, leading from the 'fecundation chamber' to the widened 'vesicle' at the base of the spermathecal 'lagena', which we have found to be of taxonomic significance. In *Mnesarchella* species this duct portion makes 2–3 spiral turns, whereas in *Mnesarchaea* it makes less than two full turns.

Remarks. The morphological interpretation of the female postabdomen in Lepidoptera remains difficult, and conditions in the Hepialoidea are particularly intriguing. With mnesarchaeids the sheer size of the ovum is a major factor determining the transfer of sperm from bursa to ovum which warrants further study.

CIRCULATORY AND RESPIRATORY SYSTEMS. The most noteworthy feature of the mnesarchaeid circulatory system is the dissociation of the metathoracic aorta from the pulsatile diaphragm below the metascutellum (Nielsen & Kristensen 1996). A similar situation was reported from a hepialid by Krenn and Pass (1995), and it was shown by Nielsen and Kristensen to be a groundplan autapomorphy of the Neolepidoptera.

Krenn and Pass (l.c.) drew attention to the retention, in the hepialid examined, of a slender 'muscular cord' linking the aorta to the metanotal pulsatile diaphragm; a similarly tenuous muscular connection is distinguishable in mnesarchaeids. While this muscular connection could be construed as an exoporian autapomorphy, it is perhaps more likely that it is a vestige of the contiguity of the aorta and diaphragm in non-neolepidopteran moths; in this case it would be described to the neolepidopteran ground plan, and its absence (if confirmed) in the Heteroneura would be a groundplan autapomorphy of this clade.

A study of the mnesarchaeid tracheal trunk configuration is outside the scope of the present treatment.

LARVAL MORPHOLOGY (Figs 109–116, 121–133)

The following account is based on *Mnesarchella acuta*. There are two reasons for largely neglecting comparative details; first, all mnesarchaeid larvae are remarkable uniform and second, the specific identity of most larvae cannot be guaranteed. They are difficult to keep alive for any length of time so that breeding adults as a means of identifying larvae is impractical. It has been achieved only with *Mnesarchaea hudsoni*, *Mnesarchella acuta* and *M. fusilella*. At the level of this description, no morphological differences have been detected between the larvae of *Mnesarchella* species. On the other hand, larvae of *Mnesarchaea*, which have been identified from unambiguous collection localities, can be discriminated by morphological characters.

The following description of larval morphology is given in some detail since this is the first such description following a brief outline by Gibbs (1979). In general they most closely resemble other hepialoid larvae where these are known, sharing features of habitats and behavior as well as structure. A discussion of larval synapomorphies is included.

Description. Elongate larvae (length:width ratio 16:1) capable of active wriggling movements and with a highly mobile head. (Figs 20, 24, 25, 109.) The trunk maintains its greatest diameter along the first six abdominal segments from whence it tapers towards each end. Mobility of the thoracic segments is aided by forward tapering such that the prothorax is only about 0.7 of the first abdominal segment. The integument is unicolorous, soft and generally without pinacula except for the prothoracic and anal 'shields'. Small irregular pinacula occur in some species on the dorsum of the thoracic segments in association with the D2 and SD setae. The body wall is thrown into numerous folds and creases of importance in relation to the position of setae and their function (Fig. 124). In all instars except the first, the integument is densely studded with microsetae, each one acute and rising from a bulbous base (Fig. 130). The microsetae are melanised in *Mnesarchella* larvae, and in *Mnesarchaea fallax* and *paracosma*, giving a distinct velvety texture to the cuticle, and are clearly visible in the light microscope at x100 whereas in *fuscata* and *hudsoni* they are unmelanised, imparting a granular texture when viewed under the light microscope. Their form, however, is the same throughout.

The thoracic legs are well-developed, and typically lepidopteran, each with a U-shaped coxa and 4 tubular segments terminating in an elongate single claw. Each pair of prolegs arises from a prominent, expanded transversely oval ventral dome situated posteriorly on the segment and bearing the SV and MV3 setae around its anterior and lateral margins (Fig. 114). The cylindrical proleg is twice as long as wide, unmelanised, and devoid of setae or microtrichia (Fig. 133). Its biordinal crochets are arranged in a biserial circle, the outer circle bearing smaller crochets, half the length of longer crochets and placed in between the longer ones (Fig. 132). Larvae of *Mnesarchella acuta* and *fusilella* have about 9 macro-crochets in their first instar, gaining one more at each early moult to reach about 11 in the 3rd. instar but increasing to 14–19 in the final instar. Larvae of *Mnesarchaea* species

possess 22–29 macrocrochets in their final instar. The non-hooked, crescent shaped crochets in a circular layout provide poor grip on both rough and smooth surfaces (i.e. leaves or stems of vascular plants), but are ideally suited to engage in the silk network of the larval tunnels when extended by turgor pressure, and to disengage when the planta retractor muscle contracts. Similar biserial crochets on the anal prolegs are arranged in a semi-ellipse with a gap around the posterior side of the planta.

The abdominal spiracles are extremely basic with a simple circular cone-like raised peritreme rim (Fig. 130). Their opening is circular, no filter is visible. As in other Lepidoptera the 8th abdominal spiracle is slightly larger than the preceding ones. On the prothorax the spiracle is situated at the anterior end of a small pinaculum, devoid of microtrichia (Fig. 129). Its opening is circular but not raised as on the abdomen and is protected by a simple flap-valve.

The head is essentially prognathous and somewhat egg-shaped, being narrowed forwards and slightly flattened (Figs 121, 122). It is smooth and often, but not invariably, the ecdysial suture is present in all instars including the first, but is not visible externally (Fig 121). The post-occipital region is well developed as a wide heavily melanised flange dorsally, where it is usually retracted under the prothoracic shield as in Fig 121. Below the postocciput and behind the genal microsetae there is a deep notch in the posterior margin of the head capsule, associated with the vertical occipital muscles. Six stemmata on each side are arranged in 2 groups, a postero-dorsal row of 3 situated on an arc midway between setae A2 and SO3; and an anteroventral triangular cluster close to the antennal socket (Fig. 111). The tentorium is weakly developed (? present) but an anterior tentorial pit can be detected at high magnification (SEM x12,000) immediately alongside 'pore' Fa (Fig. 123) which is actually a small domed campaniform sensilla. The 'oral frame', recognised in hepialid larvae (Nielsen & Kristensen 1989; Dugdale 1994), is evident in mnesarchaeid larvae but takes a rather tortuous route in the vicinity of the anterior mandibular articulations. This frame surrounds the anterior and lateral margins of the head capsule, providing support at the level of the mandibles. It forms a bridge across the front of the antennal socket, between the anterior and posterior mandibular articulation points, but with a small unmelanised notch (the "lateral slit") beside seta SO1 (Fig. 111) and another notch in the antero-dorsal corner of the antennal socket. At this latter point, more or less directly over the anterior mandibular articulation, the oral frame is distinctly stepped forward resulting in the anterior margin of the clypeus being carried forward well over the mandibles. An entirely unsclerotised anteclypeus is flexible and permits the labrum to be partially retracted. The labrum is strongly curved in lateral view so that it bends down almost at right angles to the clypeus, completely covering the mandibles (Fig. 111). There are 5 pairs of setae on its outer surface and 3 pairs of elongate flattened sensory 'cones' on the epipharynx.

The antenna is extremely shortened, reminiscent of the generalised condition in leafminers (Dethier 1941). The antecornia arises from an almost circular "socket" in the head capsule. There are two very narrow ring sclerites comprising the 1st and 2nd segments. The first is incomplete and the second supports a long and a short seta, together with five other sensory structures (Fig. 125). The latter comprise 2 long tapering tusk-like basiconic sensilla with spiral texture, on opposite sides of the antenna, with the remaining three elements on the reduced third antennal segment situated on the mesal side. One element is a tusk-like basiconic sensillum similar to those on the 2nd segment, the others comprise a long sensillum (equal to the "tusk") and a minute hair-like sensillum on a common base.

Each mandible carries a single long tactile seta on its outer face near the anterior articulation, with a campaniform sensillum above it. There are five clearly defined cusps, four roughly equal, and a shorter ventral cusp.

The maxilla-labium complex closely resembles that of Hepialidae, except that the palps and spinneret are greatly elongated (Figs 111, 112, 122). The maxilla comprises a darkly melanised cardo prominently articulated with a more lightly melanised stipes which bears two distal segments, the terminal one carrying the palp laterally and the maxillary lobe medially, both with a common sclerotised base. The palp is two-segmented, each segment as long as the lobe, with a truncate terminal apex bearing a minute bristle and basiconic sensilla. The maxillary lobe bears two short setae, three long sensory cones and four shorter sensilla. The labial submentum is an undivided, very lightly melanised plate situated between the two cardo elements, all three components together being arched to form a prominent transverse ridge across the back of the maxillo-labial complex. A pair of long tactile setae occurs on a narrow transverse sclerite situated on the proximal third of the largely unmelanised mentum, with a medial patch of scales distal to the setae. The prementum is strongly melanised, and bears the spinneret (roughly

equal in length to the mentum), which is flanked by a pair of long setaceous palps. The latter consist of two extremely elongate segments, extending to over half the length of the spinneret, the distal one grooved longitudinally. At the base of each palpifer is a minute seta on the outer side of the prementum (Fig. 112).

Chaetotaxy (Figs 110–116). The following description stresses hepialid comparisons. It is unfortunate that the larval stages of ‘non-core’ Hepialidae are not yet available for comparative study, thus diminishing the phylogenetic value that can be placed in these characters.

The nomenclature used here follows Hasenfuss (1963, 1969) with the exception of the genal seta G2 where Hinton's (1946) terminology is retained and the interpretation of the trio of prothoracic setae (D2, SD2 and SD1), which follows Wagner (1987), Dugdale (1994) and Grehan and Rawlins (2003).

On the head five distinctions from Hepialidae are evident (Figs 110–112). 1. In the V group, the ‘pore’ Va is absent, but the long macroscopic and two minute setae are hepialid in position. 2. The L seta is present, but La is not. 3. In the O group, seta O2 (Hinton's O3) occupies a unique position closer to the antennal socket than the most posterior stemma. 4. The genal area bears two minute proprioceptor setae, G2 and G2 as in Hepialidae, but the pore is absent. 5. On the frontal area, pore Fa is ventrolateral to seta Fl and some distance from it (Fig 110), a distinction from the hepialid position in which the seta is immediately medial to the pore. The above features are consistent in all examples of *Mnesarchaeidae* examined. It should also be noted that three undesignated pores occur around the antennal socket, one posteriorly and two close together ventrally.

The trunk segments shown in Figs 113–116 feature some minor but important distinctions from Hepialidae. On the prothorax the dorsal pinaculum (‘prothoracic shield’) shares many features with Hepialidae. Its anterior edge bears the same setae with the exception that D1 is set back from the edge and thus ‘behind the front line’ of setae. Distinctive sunken ‘pores’ occur in front of D1, and another between XD1 and XD2 (Fig. 128). L3 is well off the margin of the shield in *Mnesarchaea* (Fig. 115); but very close to it, occasionally connected by a melanised strip in *Mnesarchella* (Fig. 113). The most notable character, shared with Hepialidae, is the specialised development of the two SD setae, SD1 and SD2, on the prothoracic shield. These setae become thinner than the normal macrosetae after the first moult, a condition referred to as ‘filiform tonosensilla’ by Grehan and Rawlins (2003), with more flattened bases (Figs 126, 127). Seta D2, which lies between SD1 and SD2, remains a normal macroseta (Fig. 126). All three posterior shield setae are surrounded by an oval microtrichiated area lying along the posterior margin of the prothoracic shield and continuous with the soft cuticle, except that the microtrichia are more elongated in comparison with those on the soft cuticle as shown in Fig. 126. An almost identical specialisation of SD1 and SD2 and their association with D2 occurs in *Aenetus*, *Endoclita*, *Phassus* and *Zelotypia* (Hepialidae) (Grehan & Rawlins 2003; Simonsen 2018). Variations on a similar theme occur in all other known hepialid larvae (Grehan 1981, Nielsen & Kristensen 1989, Dugdale 1994). The prothoracic proprioceptor seta MXD1 is absent in *Mnesarchaea* as it is in Hepialidae. However, MV3 is represented on *Mnesarchaea* as a minute proprioceptor, never a macroscopic seta associated with MV1 on a pinaculum as occurs in Hepialidae.

The large transverse folds of integument on the remaining segments are useful landmarks for describing setal positions and are indicated on the chaetotaxy map (Fig. 113). Several small creases occur between segments with either one or two major ridges around the centre of the segment. On the meso- and metathorax, where two major ridges occur dorsolaterally, the D1 and L2 setae are on the anterior one whereas D2 and all setae below it are on the posterior one. On these segments D2 is longer than D1; and between them in the thinner cuticle of the fold between the two major dorsal ridges, can be seen the attachment point of the chordotonal organ (Fig 131) (Hasenfuss 1963). On the mesothorax of examined *Mnesarchella* larvae, SD1, SD2 and D2 are situated on a common but very irregular pinaculum, while on the metathorax, only SD1 and SD2 are so combined. However, the occurrence of these pinacula is quite variable. A mesothoracic pinaculum containing D2 and SD2 appears on some *Mnesarchaea* larvae but the metathoracic pinaculum is absent. The trio of microscopic proprioceptor setae, MD1, MSD1 and MSD2 are situated on the intersegmental ridge, not associated with pinacula. As in Hepialidae, L2 is anterodorsal from L1, and MV3 is minute on the mesothorax but a longer tactile seta on the metathorax. Immediately posteroventral to seta L1 can be seen the pit of the developing wing bud. The proprioceptor MV1 is situated in a fold which has contact with the preceding coxal ridge, while MV2 and MV3 are well back on the major integumental fold which bears the coxa.

On the abdomen the major transverse ridge is slightly anterior on each segment and carries the D1 seta dorsally, with the SD group, spiracle, L2 and L3 below it (Fig. 113). The D2 seta, equal to or slightly shorter than D1, is on the more posterior ridge. The prolegs are on a raised ventral dome situated posteriorly on the segment, roughly below D2. Seta MD1, somewhat longer than a typical proprioceptor, is situated in a thin area of integument which folds during movement (Figs 114–116). From A1 to A8 the pair of SD setae are close-set on a small pinaculum between D1 and the spiracle. Unlike in the Hepialidae, but more typically of Neolepidoptera, SD2 is very short, less than 1/10 of SD1 (Fig. 124). The attachment point of the chordotonal organ (Fig. 131) is visible on the integument posterodorsal from SD2 (Fig. 114 ch). L3 is anterior to or on the vertical line through the spiracle. The SV group comprises 3 setae more or less in line around the outer side of the proleg base or "ventral dome" in *Mnesarchella* larvae and *Mnesarchaea fallax* but an additional SV seta occurs posterior to SV3 and at right angles to the line of the others in *Mnesarchaea paracosma*, *fusca*, and *hudsoni*. Only two SV setae occur close together on segments A7–9 in all species. As in Hepialidae, the normally microscopic MV3 seta is elongate on segments A2–7, but minute on A1 and A8–9. The anal shield is a prominent area, free of microtrichia and bearing three pairs of setae and one pair of pores. Two setae and a pore occur on each subanal plate, while around the anal proleg the anterior pinaculum bears 3 setae and posterior pinaculum 2.

INSTAR CHANGES. Setal positions and overall shape do not differ sufficiently to justify a separate description for the first instar. On the head capsule all setae and pores are present from hatching, but on the trunk the L group and SV group contain subprimary setae that do not appear until after the first moult. Thus on the meso- and metathorax of the first instar larva, L2 is absent and on all segments; L3 is also absent. Within the SV group similarly SV2 is absent on the meso- and metathorax while SV3 is absent on all segments until after the first instar. Where a fourth SV seta is present on the proleg base (as in *Mnesarchaea paracosma*, *fusca*, *hudsoni*), it appears only after the first moult. On A9 of second instar larvae, a new seta appears in front of SD1 which, because of its length and subprimary status, Hasenfuss (1969) argues is not SD2.

The cuticular microsetae are essentially absent from first instar larvae, although a few can be seen near the dorsal mid-line on the posterior abdominal segments and around the bases of the prolegs. In the second and subsequent instars, microsetae densely cover the trunk cuticle with the exception of the pinacula.

Remarks. In the early days of this study, the strong similarity between mnesarchaeid larvae and those of the then known hepialid larvae was taken as evidence of a close affinity between these two families (Gibbs 1979). Detailed evidence presented here amply supports this relationship, now confirmed by recent molecular analysis (e.g. Regier et al. 2015). A point has been reached where it is reasonable to predict that when the larvae of *Anomoses*, *Neotheora*, *Palaeoses* and other 'non-core' hepialid groups are described, they will be found to comply with the patterns described here.

Identification of larvae. More than 80 mnesarchaeid larvae have been examined from 15 different sites around New Zealand extending from the Waitakere Range (AK) in the north to Fiordland (FD) and the Takitimu Range (SL) in the south, to draw up the descriptions. The overall impression is that they are remarkably uniform in structural details but show some quite marked differences in the colour of their living cuticle. It has been possible to find 10 characters that are of some value for discriminating between larval types, enabling five larval taxa to be recognised. Since molecular association of larval types with adult taxa was not practical during most of this study, identification was inferred largely from their collection sites. Further study to differentiate between larval taxa clearly requires DNA characterisation.

Nevertheless, one thing is clear: the colour of living larvae provides a straightforward means of distinguishing between the two genera: *Mnesarchaea* larvae are bright green whereas *Mnesarchella* species vary between olive brown and dark grey (Figs 24, 25). All traces of cuticle colour disappear after preservation in alcohol. A key to larval taxa is given in the Systematics section and descriptions follow with each species.

PUPAL MORPHOLOGY (Figs 117–120)

Pupae of *Mnesarchella acuta*, *M. fusilella* and *Mnesarchaea hudsoni* have been examined. The pupa is shortened in comparison with the larva, with a length ratio of only about 4.5 x head width. Its integument is virtually colourless, unmelanised except for the spines and some of the more robust sutures which are pale brown. The leaf-green pigment of living *Mnesarchaea* larvae is carried through to the pupa. The extremely thin and flexible integument makes it difficult to determine which inter-segments are "fixed" and which articulate. We have interpreted the abdominal articulation as involving segments 1–6 as indicated on the diagrams (Figs 117, 118). The legs, wings and antennae are only weakly cemented together and tend to separate in preserved specimens, but since exuviae retain these as a single unit, it is assumed that separation does not occur in life.

The head carries two blunt melanised cocoon-cutters on the mid-line in the frons region. The dorsal one, situated between the antennal bases, is bilobed in *Mnesarchella fusilella* and *acuta* but single in *Mnesarchaea hudsoni* while the ventral one, at the antero-ventral extremity of the pupa is single in the examples seen. Five pairs of tactile setae occur on the head of *Mnesarchella acuta* and *Mnesarchaea hudsoni*; one pair on the vertex, two pairs on the frons lateral to the dorsal cocoon-cutter and two pairs on the clypeus. A sixth pair is present in *Mnesarchella fusilella*, longer than the others and situated across the frons between the median cocoon-cutter and the clypeus. The mandibular sclerites are clearly delimited, slightly bulbous, each with a single seta. Sheaths for the galea are characteristically turned inward over the coxae of leg I and meet in the mid-line at about two times the length of the labial palps. There is a small transverse sheath for the maxillary palp. In the male the antennae are longer than leg II, reaching to the margin of A5 but in the female only to the end of leg I. The forewings reach to the middle of A5 in *Mnesarchella acuta* and *fusilella* but to the rear of A6 in *Mnesarchaea hudsoni*. In *acuta* and *fusilella* (but not *hudsoni*) each forewing is bent abruptly outwards at its extreme apex and lightly melanised to form a spine of similar size to the ones near the base of the forewings (see below). There is no trace of proleg scars on the abdomen. The pattern of abdominal setae is shown in the diagrams (Figs 117, 118). The only segments with a full compliment of setae are A6 and A7. The SD group is represented by only a single seta throughout. Circular spiracles occur on segments A2–A7 with a non-functional vestige on segment 8 (although there is a tracheal connection left in the pupal exuviae).

On the dorsum, the prothoracic spiracle is visible as an oval slit with a comb-like filter between the pronotum and the forewing margin. There is a prominent lateral retro-spine on each forewing sheath just behind the level of the eyes and a series of mid-dorsal abdominal spines from T3 to A8. The latter vary in form as follows: T3 is a simple blunt median crest; A1 an insignificant crest; A2 a low crest near front of segment; A3–A6 each with the median crest together with a pair of spines immediately anterolateral to it, the spines becoming progressively longer and more backward sloping toward A6; A7 with an anterior double spine and a larger median posterior spine (double in *hudsoni*); A8 lacking the anterior spines but with a stout erect anterior-directed spine; A9 with neither spines nor cremaster but in *acuta* (not *fusilella* or *hudsoni*) bearing 2 pairs of setae on its dorsal half.

Segments A8 and A9 show sex differences as illustrated (Figs 119, 120). In the male the gonopore is visible as a pair of semicircular mounds on the sternum of A9. There is a bilobed terminal projection bearing the anus in both sexes but it is more pronounced in the female. The midventral margin of the 9th sternum is pulled forward, signifying the proximity of the gonopore in the female.

The pupal morphology implies it is of the type which partially escapes from the cocoon before emergence. However, not all do this—emerged cocoons (of *M. hudsoni*) have been found with the exuviae left entirely within the cocoon. The presence of anterior cocoon-cutters, a pair of lateral, backward-facing spines, the series of backward-facing mid-dorsal abdominal spines and the large terminal dorsal spine which faces forward, combine to permit extrusion of the anterior part of the pupa while ensuring that it remains anchored within the silken cocoon posteriorly. The pupal exuviae are left in a wrinkled state with segments A2–6 telescoped and the wings and appendages projecting as an unsupported unit. The cuticle splits across the vertex between the frontal setae and the vertex setae, along the antennal sutures and down the centre of the meso- and metanotum, leaving the rest of the head and the ventral appendages intact.

Nielsen and Kristensen (1989) reviewed the known exoporian pupae and recognised four basic types, three of which are hepialid (*s. lat.*) and distinguished by the nature of the transverse bands of cuticular spines on the abdomen, the fourth is mnesarchaeid. Expressed in this way, the mnesarchaeid pupa differs greatly from the other

known pupae in the Hepialoidea (*Prototheora*, *Fraus*, *Gazoryctra*, and Hepialidae *s.str.*). Its most significant characteristics are the thin, non-sclerotised integument, the resulting freedom of movement, and the absence of abdominal comb-like rows of spines; even the chaetotaxy differs markedly. Some of the distinctions may be related to its small size and more "delicate", humid habitat (but there are large hepialid larvae that live in wet moss (see Grehan & Patrick 1984)).

Hinton (1946) predicted that the archetypal pupae of Endopterygota had a thin and flexible cuticle and functional jaws. This implies such a state is primitive and that the other exoporian pupae are therefore more specialised. The mnesarchaeid pupa lacks functional mandibles (although it possesses a mandibular sheath). Hinton (1946: p. 292) remarked that "it seems certain that the lepidopteran pupa never passed through the stage represented by the pupa of recent Coleoptera and Hymenoptera, that is, of being free and without functional mandibles. No transitional forms are known between the pupae of *Dacnonypha* and the obtect pupae of *Monotrysis* and *Ditrysis*". Mnesarchaeid pupae could be described as fitting that intermediate stage to some extent: their appendages remain fused together as a unit. But there is little doubt that the middle region of the abdomen, in the vicinity of segments 4–5, can flex considerably without any constraint from the appendage sheaths which project freely from it. This would aid the pupa's locomotory potential, using the tips of leg III as a lever, but the action is restricted in comparison with a truly mobile exarate pupa with functional mandibles. Regier et al. (2015: p. 20) draw attention to two species of *Ogygioses* from Taiwan, another small hepialoid that constructs silken tunnels within a mossy substrate, but the larval and pupal morphology is yet to be described.

SYSTEMATICS

FAMILY DIAGNOSIS

ADULTS (Figs 1–18): Mnesarchaeidae are by far the smallest of the Hepialoidea with forewing lengths of 3.1–5.5 mm and the only ones with functional mouthparts in the adult. Family autapomorphies include: the **narrow, lanceolate** forewings (Figs 56, 57) with length/width ratio of 3.7–4.0; **Rs1+2 in both wing pairs represented by a single vein only**; Rs3+4 uniquely sharing a common stem with M1 in half the species; the **fork of RS3+4 very characteristically symmetrical about the apex**. Wing coupling mechanism essentially non-existent, purportedly interlocking fringes of hairs on both wing margins (Fig. 49) (although a vestigial jugal lobe remains, we believe the wings beat independently). Sternum A1 bilobed (Fig. 47), with external arms; male genitalia (Figs 59–64) with anteromedial process of valva synscleritous with anterolateral corner of the pseudoteguminal plate—resulting in a spacious subgenital crypt which can hinge open to accommodate the female genital plates; female genitalia (Figs 98, 99) with elongate, anteriorly synscleritous subgenital and dorsal plates.

For practical purposes they are best recognised from other small moths in this country by their combination of: 3-segmented labial palps; long (0.5–0.7x forewing length in male), unadorned antennae of 31–43 flagellar segments, 28–37 in female, **held erect and divergent in life**; spurs present on middle and hind tibiae, and the venation patterns shown in Figs 56–57.

IMMATURE STAGES: Larvae broadly as other hepialoids, but with a more specialised body-form (Figs 24, 25, 109), elongate, reaching a maximum of 10 mm in total length at maturity, with the thickest region between segments A1 and A6, tapering towards either end. The larva is adapted for life in silken tunnels—highly mobile, semi-looper style, moving in either direction; proleg crochets crescent-shaped but not hooked, biordinal, arranged in two concentric circles. Head prognathous, with an **exceptionally long spinneret**. Chaetotaxy essentially hepialid with a notable specialisation on prothoracic shield margins of setae D1, SD1 and SD2 (Fig. 126). Cuticle unicolourous, green (*Mnesarchaea*) or brownish to dark grey (*Mnesarchella*), with a velvety texture due to dense covering of microtrichia (Fig. 124). Chaetotaxy presented in Morphology section.

The larva constructs a silken web of tunnels throughout the open spaces within the thick green periphyton layer of wet rainforest. It feeds on moss leaves, hepatics, algal cells, fungal hyphae in this layer and is able to move rapidly along its tunnel system. A loosely woven silken pupal cocoon is formed within the tunnel network (Fig. 21 arrow). The pupa (Figs 117, 118), is small (3–5 mm) with a flexible, unsclerotised cuticle, hence only minimal spination on the abdomen. The pupa lacks functional mandibles (adecticious), as do all exoporians and the other appendages remain fused together as a unit at emergence. Its mobility arises from abdominal flexibility.

KEYS TO ADULTS

Below are three keys for the identification of *Mnesarchaeidae* species, each designed for different categories of specimens. Thus A is intended for use with pinned museum specimens or any material that retains the scale covering and colours of living moths. The other two keys (B and C) apply to male and female separately and are targeted at the use of genital preparations for confirmation of species identity. Male genitalia offer a discrete range of unambiguous characters to clearly discriminate between the 14 species; female genitalia much less so, but females are rarely encountered in collections. Note that geographic locality data are included here as a guide for identification, remembering that locality cannot define the species entity – the history lesson from *mnesarchaeid* identification is that only by diligently examining male genitalia from each location will proper taxonomy be carried out or new taxa revealed.

A. External features—superficial key for dry specimens

1. Forewing with a strong dark brown costal streak between costa and R vein to about 1/2–2/3, backed by whitish ground colour in cell (Figs 17, 18)..... 2
- Forewing without a distinct costal streak, wing ground colour ochreous, pale brown or dark brown (Figs 1, 7, 16) 6
2. Costal streak terminates obliquely at R with an inwardly acute costal angle (Fig. 17) 3
- Costal streak terminates obliquely at Sc with an outwardly acute costal angle, its apex curved inward around the end of the cell—the *acuta*-group of 7 species (Fig. 9)..... 4
3. Scales under head (on postmentum and prosternum) dark brown; an oblique dark brown streak extends across anal area from eye to end of anal vein on dorsum; tegulae brown (N.I. and northern S.I.) (Fig. 18)..... *Mnesarchella loxoscia*
- Scales under head white; anal area of forewing white except for a small patch of brown scales on dorsum at about 1/4; tegulae white (N.I. only) (Fig. 17) *Mnesarchella fusilella*
4. Anal margin of forewing between head and beginning of fringe scales at CuA lacking any trace of a brown fascia (Fiordland) (Fig. 13) *Mnesarchella philpotti*
- Anal margin of forewing with an irregular oblique patch of brown scales about half way between head and fringe scales 5
5. Long fringe scales arising from anal margin of forewing at CuA1 (beginning of tornal fringe) dark brown (Fig. 12) *Mnesarchella ngahuru*
- Long fringe scales arising from anal margin of forewing at CuA1 white—forming a white band across the fringe at this point (Fig. 10)..... **all remaining *Mnesarchella* species: *acuta*, *falcata*, *hamadelpha*, *stellae*, *vulcanica***
6. Forewing ground colour predominantly pale brown or ochreous 7
- Forewing ground colour predominantly dark brown 8
7. Forewings uniform pale brown with a brassy iridescence, a narrow white transverse line at 4/5 and a band of white scales along the termen and dorsum (northern and central N.I.) (Fig. 16) *Mnesarchella dugdalei*
- Forewing predominately ochreous but with diffuse brown, white and yellow scale patterns (eastern and central S.I.) (Fig. 7)..... *Mnesarchaea paracosma*
8. Scales on antennae, head and palps ochreous-brown; forewing length 4.0–4.5mm, 3 or 4 small white scale patches across middle and on margins at base of fringe, otherwise entirely dark brown; fringe scales dark brown (central N.I., Mt Taranaki and Nelson) (Fig. 1) *Mnesarchaea fallax*
- Scales on antennae, head and palps ochreous-yellow; forewing length 3.2–4.1mm, spangled with ochreous scales, fringe scales of termen with dark brown and ochreous bands 9
9. A small species, forewing length 3.2–3.5mm; male genitalia with a pair of heavily sclerotised dorsal processes with out-turned tips (northern S.I. only) (Fig. 3) *Mnesarchaea fusca*

- A larger species, forewing length 3.4–4.1mm; male genitalia with a pair of straight spear-like processes projecting from centre of genital field (often visible on dried specimens) (N.I. only) (Fig. 5)..... *Mnesarchaea hudsoni*

B. Key based on Male Genitalia

1. Vinculum of variable form, never crescent-shaped (Figs 79, 80, 82); A10 lobes absent or poorly defined
Mnesarchaea: 4 species 2
- Vinculum crescent shaped with anterior margin smoothly convex (Fig. 64); a pair of finger-like setose dorsal A10 lobes (Fig. 63) *Mnesarchella*: 10 species 5
2. Pseudoteguminal plates bearing 1–3 pairs of long sclerotised, acutely pointed processes ('periphallic arms') projecting posteriorly from the dorsal region of the genital capsule (Figs 66–68)..... 3
- Pseudoteguminal plates supporting 1 pair of short, thick membranous subanal 'periphallic arms' (Fig. 65) but otherwise lacking long posterior processes *fallax*
- 3.Periphallic arms strongly asymmetrical (Fig. 68) *paracosma*
- Periphallic arms symmetrical 4
4. A single pair of thick crescentic subanal periphallic arms arising from below the anal cone, their pointed apices bent outwards (Fig. 66) (northern S.I.) *fusca*
- Three pairs of long thin periphallic arms; the medial subanal pair straight, twice length of two lateral pairs of arms that curve outwards, (Fig. 67) (N.I. only) *hudsoni*
5. Dorsal surface of ventral valve lobe with the setae unspecialised, not melanised, i.e. lacking a clearly defined pecten (Figs 86, 88)..... 6
- Dorsal surface of ventral valve lobe with a clearly defined patch or comb-like row of strongly melanised bristles (pecten) (e.g. Figs 84, 85) 7
6. A large species, forewing >4.3mm; dorsal arm of valvae with a club-like apex bearing about 5 blunt melanised teeth around the margin (Fig. 88) (NW Nelson)..... *stellae*
- A small species, forewing <4.1mm; dorsal arm of valvae lacking marginal melanised teeth (Fig. 86) (central and southern N.I.) *ngahuru*
7. Pecten bristles densely crowded into an oval patch (Fig. 83, 89)..... 8
- Pecten bristles aligned in a single comb-like row (Figs 84, 85, 87) 9
8. Pecten bristles grouped in centre of valve lobe (Fig. 83); the posteromedial angle of valve lobe acute (southern N.I. and north and west of S.I.) *acuta*
- Pecten bristles grouped very close to posterior edge of valve lobe (Fig. 89); the posteromedial angle of valve lobe a right-angle (mid N.I.) *vulcanica*
9. Pecten bristles distinctly oval in cross section; a pair of diagnostic melanised dorsal periphallic arms present (Fig. 84) (central N.I.)..... *falcata*
- Pecten bristles circular in cross section; lacking periphallic arms 10
10. Trulleum sclerotisation absent; dorsal arm of valvae with about 5 short bulbous setae near apex (Fig. 87) (Fiordland)..... *philpotti*
- Trulleum sclerotisation conspicuous; dorsal arm of valvae with normal tapered setae..... 11
11. Trulleum in form of a 'W'-shaped melanised bridge with a granulated surface texture (Fig. 91)12
- Trulleum in form of a 'U'-shaped bridge with only the tips of the U (on either side of the mid-line) melanised and spinose (Fig. 85) (central New Zealand)..... *hamadelpha*

12. Cornuti present as large acutely-pointed spines on a tear-drop-shaped base either side of the midline, often with small supernumerary spines also (Figs 90, 92) 13
 - Cornuti absent (Fig. 91) *fusilella*
13. Cornuti with double apical spines; trulleum bridge very broad (Fig. 90) (Northern N.I.) *dugdalei*
 - Cornuti with a single large apical spine; trulleum bridge of moderate width (Fig. 92) (N.I. only) *loxoscia*

C. Key based on female genitalia

Note that all characters are with reference to cleared, stained preparations in ventral view. Microtrichia (where present) adorn the exterior surface of the subgenital plate, towards the apex. Acutely pointed scutes of various form (Figs 44, 45 and insets A, B, C of Fig 104) have taxonomic significance and occur on internal walls of the antrum.

1. Abdomen tapering to a relatively **narrow** bi-lobed apex, each lobe finger-like with a deep mid-line indentation and a prominent terminal seta; subgenital plate narrow, arched, nesting into dorsal plate (Fig. 93), exposed surface devoid of scales but with a few scattered setae *Mnesarchaea* 4 species ... 2
 - Abdomen tapering to a **broad** bi-lobed apex, the lobes rounded, with a shallow mid-line indentation; floor of genital chamber (subgenital plate) broad and scoop-like, lightly melanised, sparsely clothed with scales *Mnesarchella* 10 species ... 5
2. Apex of subgenital plate very narrow, tapering to about a quarter of its width at widest point (Fig. 94) *fallax*
 - Apex of subgenital plate moderately broad (same width as antrum), tapering to less than half of its width at widest point (Figs 95–97) 3
3. Anterolateral angles of subgenital plate modified to form a pair of **deep pockets** behind sternum VII (Fig. 97) *paracosma*
 - Anterolateral angles of subgenital plate without pockets 4
4. Exposed external surface of subgenital plate densely clothed with microtrichia over its posterior half, anterior half devoid of microtrichia (Fig. 96) *hudsoni*
 - Microtrichia on exposed surface of subgenital plate restricted to a median band distally and two smaller lateral patches at anterior angles (Fig. 95) *fusca*
5. Floor of genital chamber with a V-shaped supporting sclerite along lateral margins; bursa copulatrix elongate, of constant diameter, extending full length of abdomen 6
 - Floor of genital chamber lacking a V-shaped sclerite; bursa oval, not extending full length of abdomen. (Fig. 100) *falcata*
6. V-sclerite arms connected by a distinctly melanised transverse bridge (entire or often incomplete) towards their anterior apex, adorned with prominent acutely pointed scutes 7
 - V-sclerite arms lack a melanised bridge with scutes (Fig. 107) *fusilella*
7. Anterior stem of V-sclerite strongly melanised, more or less entire (Fig. 102) 8
 - Anterior stem of V-sclerite incomplete, lacking a distinct apical piece (Fig. 104) *stellae*
8. Subgenital plate adorned with microtrichia over some or most of its posterior exposed surface (Figs 99–104, 106–108) 9
 - Subgenital plate lacking all microtrichia on its exposed surface (Fig. 105) *vulcanica*
9. Microtrichia covering entire posterior half of subgenital plate (e.g., Fig. 108) 10
 - Microtrichia restricted to lateral margins towards posterior apex (e.g., Fig. 107) 12

10. Macrotrichia widespread on apical half of subgenital plate but tend to be concentrated toward posterior apex (Fig. 106) 11
 - Macrotrichia widespread on apical half of subgenital plate but with two distinctive rows of 3 closely aligned setae, separated by a gap at the apex which lacks almost all setae (Fig. 101)..... *hamadelpha*
11. Subgenital plate bearing a small, posteriorly-directed spine on its lateral margin about half way between apex and base (Fig. 108)..... *loxoscia*
 - Subgenital plate lacking a lateral spine (Fig. 106)..... *dugdalei*
12. Scutes on antrum bridge simple, acutely-pointed, tooth-like (Figs 44, 99 inset B)..... *acuta*
 - Scutes on antrum bridge tooth-like but with multiple blunt comb-like marginal teeth (Figs 102, 103)..... 13
13. V-sclerite bridge crosses at anterior end of antrum, close to stem of V-sclerite, clearly defined and relatively narrow (Fig. 103)..... *philpotti*
 - V-sclerite bridge diffuse, crosses central region of antrum, (Fig. 102) *ngahuru*

Preliminary key to larvae

1. Colour in life leaf green; prothoracic spiracular pinaculum short, oval, seta L3 closer to spiracle than to shield margin *Mnesarchaea* 2
 - Colour in life ochreous to olive-brown or dark slaty-grey; prothoracic spiracular pinaculum elongate, pointed, seta L3 closer to shield margin than to spiracle *Mnesarchella* species (not keyed further)
2. Abdominal segments 1–6 with 3 SV setae..... *fallax*
 - Abdominal segments 1–6 with 4 SV setae..... 3
3. Microtrichia melanised, clearly visible at x100 in light microscope; head capsule yellow-brown *paracosma*
 - Microtrichia unmelanised, not visible at x100 in light microscope, although their swollen bases impart a granular texture; head capsule unmelanised..... 4
4. From North Island *hudsoni*
 - From northern South Island *fusca*

Genus *Mnesarchaea* Meyrick, 1885

Figs 1–8, 25, 27, 31, 33–4, 36, 38, 48, 50–52, 56, 59–61, 65–68, 79–82, 93–97, 115–116, 136–142

Mnesarchaea Meyrick, 1885. *New Zealand Journal of Science*, Vol 2: 591. Type species: *Mnesarchaea paracosma* Meyrick, 1885, by original designation.

Note. This genus is equivalent to the *fusca*-group of species in previous accounts (Gibbs 1979). Four species share a number of important genitalia characters which distinguish them from *Mnesarchella* species; determination confirmed by nucleotide analysis. They can be distinguished from *Mnesarchella* on colour alone as explained below.

Diagnosis (Figs 1–8). Head vestiture pale ochreous to ochreous brown, **never white**; more or less uniform, **lacking a dark brown lateral streak at eye-level**. Antenna distinctly yellowish; flagellar segments with multi-armed sensilla trichodea with 3–5 arms (Fig 33); scape brown-scaled. Thorax dorsal vestiture never whitish, varying from pale ochreous-brown to dark brown. Forewings either uniformly dark brown with scattered white or ochreous scales (*fallax*, *fusca*, *hudsoni*) or pale brown with a diffuse pattern of brown, white and ochreous scales (*paracosma*). Forewing venation with M1 arising separately from the stem of Rs4+5 (except *fusca*).

Male genitalia (Figs 38, 59–61, 65–68, 93–97). Dorsal A 10 lobes absent except for a highly modified form in *M. fallax* where the lateral extremities of the abdominal dorsum bear a concave sclerite bearing a cluster of spines. Transverse pseudoteguminal plates variably developed, but in all species bearing some form of elongate species-specific periphallic arms on either side of genito-anal field. Anteroventral arms of pseudoteguminal plates support

roof of subgenital crypt. Male gonopore in all species flanked by a pair of long subanal arms developed from the pseudoteguminal plates. In *fusca*-subgroup a presumably eversible membranous phallus is usually identifiable in phallocrypt. Cornuti absent. Subgenital crypt spacious, being effectively extended posteriorly by inner surfaces of vinculum and valvae together; central part of crypt roof largely membranous, lacking any distinctive 'trulleum' sclerotisation, but pseudoteguminal plates united by distinctly melanised bridge some distance in front of bases of peripheral arms. Discrete juxta not discernable but possibly represented by narrow wavy band of thickened cuticle on floor of subgenital crypt. Exposed distal end of valvae roughly rectangular, comprising a small finger-like piece (dorsal arm) bent sharply downwards; with piliform scales on outer surface grading into thin setae towards upper arm; setae on inner face can form a discrete patch, but never a distinct pecten. In *fallax* the entire distal valva may be folded into the subgenital crypt in repose but this has not been observed in other *fallax*-group species. Valvae separated in mid-ventral line by thickened unmelanised cuticle. Vinculum outline variable.

Female genitalia (Figs 93–97). Posterodorsal lobes in the form of two compact parallel rods, very close together, darkly melanised, densely covered with microtrichia; each lobe setose but with a distinctive single specialised seta on its outer side at the tip, arising from a thin, smooth cuticular dome. Dorsal and subgenital plates both elongate, 1.7–2.5x longer than wide, arched, and nesting into one another with a common anterior articulation across the middle of the collicular region of the ductus. Exposed ventral surface of subgenital plate devoid of scales, bearing only scattered setae and with distinctive patterns of microtrichia; posterior apex of subgenital plate broad and weakly bilobed. Collicular area of ductus lightly melanised, with longitudinal ridges or keels dividing the duct into compartments; roof close-set with spinules (sparse in *fallax*). Corpus bursae oval. Spermatheca on a short duct with only one spiral turn, with lagena.

Larva. Head capsule brownish, or almost unmelanised. Trunk unicolourous, in life bright green or greyish-green (Fig. 25); microtrichia present (except in first instar) but not visible in light microscope at x100 in *fusca* and *hudsoni* due to their lack of melanisation. Chaetotaxy: Prothorax with spiracular pinnaculum short, oval; metathorax with SD1 closer to L3 than to SD2; abdominal segments 1–6 with L2 well behind the vertical line through spiracle. Mature larva with 20–29 macrocochets in a biserial circle (*fallax* mature larva unknown).

Remarks. *Mnesarchaea* species are clearly distinguished from *Mnesarchella* species on the phylogenetic tree (Fig. 135). They are generally inconspicuous members of the fauna on account of their drab colours, restricted flight seasons and localities and their subtle habitats within or around the margins of forest. Yet on the right day, they can appear to be remarkably common. Biogeographically, they could repay some intensive molecular analysis to shed light on the geographic ranges of *fallax* (on both Tongariro and Taranaki volcanoes as well as across the Nelson district) and the disjunction of sister species *fusca* and *hudsoni*, across Cook Strait.

***Mnesarchaea fallax* Philpott, 1927**

Figs 1, 2, 38, 48, 56, 59, 60, 61, 65, 79, 94; 136, 137, Map 1.

fallax Philpott, 1927a, p. 709 (*Mnesarchaea*); Philpott 1927b, p. 713 (*Mnesarchaea*); Hudson, 1928, p. 367, no figure (*Mnesarchaea*).

Diagnosis (Figs 1, 2, 38, 136, 137). A uniformly dark brown species with several small **white** spots across the middle of forewing and on the costa near apex; male genitalia with a pair of **club-like largely unmelanised subanal arms** but lacking other long posterior processes. Similar species: *fusca*, *hudsoni*.

Male (Figs 1, 136). Head vestiture ochreous-brown, darker on gena and vertex. Antennae long, 0.73 of forewing with 39–43 flagellomeres; scape pale brown, pedicel and flagellar scales ochreous-yellow to ochreous-brown, darker toward tip. Thorax dorsal vestiture ochreous-brown; tegulae dark brown. Forewing 4.0–4.5 mm, length/width ratio 3.8; uniformly dark brown with purple-golden reflections and a few small white marks, some of only a few scales: a small patch of white scales near dorsum at 1/4; another on tornus at 1/2 (end of cubital fold), a few scattered white scales across centre at end of cell; two small subapical patches of white scales at 4/5, one on costa, the other on tornus, sometimes joined as a fascia. Fringes same colour as wings, with a few white scales in base of fringe at 1/2 on forewing tornus. Hindwing uniform brown with purple-golden reflections, very slightly paler than forewing. Prosternum brown; legs ochreous, but brown where exposed, distal bands on tarsal segments indistinct or absent; tibial spurs brown, spines ochreous and ochreous-brown. Epiphysis present, long. Abdomen silvery brown above and below, including genital fringe.

Female (Figs 2, 137). Antennae 0.54 of forewing with 31–34 flagellomeres. Forewing 4.0 mm, white maculation more prominent than the male, with white scales forming an interrupted fascia at 1/2, a distinct

transverse fascia at 4/5, a white patch posterior to the cell and another connecting the two transverse lines near the termen. Hindwings pale grey.

Male genitalia (Figs 59–61, 65, 79) (6 preparations). Pseudoteguminal plate extends across roof of the subgenital crypt, forming a transverse dorsal shelf, lightly melanised across the shelf but with a concave melanised sclerite at each lateral extremity bearing a **cluster of 9–15 short posteriorly-directed spines**. Dorsal to the spinose plates are the unsclerotised microtrichiated 10th abdominal lobes. **Subanal periphallial arms short, parallel, in the mid-line, extending posteriorly to about the same distance as valvae**. These are largely unmelanised apart from a pair of lateral supporting sclerites; the apices textured with microtrichia. Subgenital crypt deeply cup-like, bulbous anteriorly; supported across its roof by the broad anterolateral arms of the pseudoteguminal plate which converge slightly and merge to form a transverse 'bridge' close to the point of fusion with the anterior valva extension; the lateral walls and floor of the crypt supported by the complex anterior arms of valvae and vinculum together. Valva roughly rectangular, convex on outer face but with a distinct longitudinal keel along inner face; with a finger-like dorsal arm abruptly bent downwards; both arm and distal end of keel darkly melanised; inner surface smooth except for about 20 thin setae along keel. Vinculum slightly wider than long in ventral view but with long anterior lobes extending dorsally up the side walls of the subgenital crypt; anterior margin deeply concave. (Genitalia slide G448, Upper Maitai Valley, GWG. NZAC.)

Female genitalia (Fig. 94) (1 preparation). Dorsal lobes 0.2 of total dorsal plate length; the dorsal plate slender with a maximum width near point of articulation of 0.4 of its length. Subgenital plate reaching to 0.7 of the dorsal plate length, narrow with a maximum width of 0.4 of its length; anterior margin straight with simple lateral hinges; posterior apex very narrow, notched in mid-line; each terminal lobe with a long stiff seta on its lateroposterior corner, arising from a distinctive basal cone; microtrichia present over proximal half of sternite but not at apex. Antrum extending only about 1/4 as far anteriorly from subgenital plate articulation as it does posteriorly; with a longitudinal flange along each side in region of hinge; and a median vertical partition in anterior section, roof with small delicate crenulate spinules; floor lacking spinules. Ductus without spinules. (Genitalia G443 in glycerine, temporary mount, Erua track, GGNZ.)

Larva (putative second instar). Cuticle in life bright green, concolorous with brown head capsule and pinacula. Microtrichia melanised, visible at x100. Chaetotaxy: Prothorax with L3 very close to lateral margin of shield, connected to it by a narrow neck of pinaculum; abdominal segments 1–6 with 3 SV setae present.

Type data. Holotype male, Mt Arthur Tableland, 10 Dec 1928, A. Philpott. NZAC.

Material examined. Type specimen plus 33 non-type examples (28 males, 5 females and 2 immature larvae presumed to be of this species, NZAC, MONZ, GGNZ). See Appendix 1 for list of collection localities.

Distribution. TK, TO / NN, BR.

Flight Season. 27 October to 10 December.

Remarks. Exceptionally undistinguished in its appearance and often found near water, *fallax* looks very like a caddis in life, apart from its erect antennae. It has been found in open beech forest, dense podocarp forest and amongst red tussock and flax usually at considerable elevations (260–1300 m). Although normally hard to find, aggregations of both sexes have occurred (at Lewis Pass in *Fuscospora solandri* / *cliffortioides* forest (GWG) and on Harwood's Hole track, Canaan (R. Hoare pers. comm.)) associated with dense lichen-covered tree trunks and shrubs in the understorey, thus raising the possibility that larvae might be lichen-feeders. However, the putative larvae of this species were collected in September from ground-cover periphyton at Lewis Pass, but were only in the second instar. Since adults fly at that site in late November, it suggests that perhaps this species has a two-year life cycle. Although very like the other dark brown species, *fallax* can be recognised by its small discrete markings being white rather than yellowish, and by its longer wings. Also, its flight season, so far as is known, does not overlap with either *fusca* or *hudsoni*.

***Mnesarchaea fusca* Philpott, 1922**

Figs 3, 4, 66, 80, 95, 138, 139; Map 2.

fusca Philpott, 1922a, p. 8 (*Mnesarchaea*); Philpott 1927b, p. 712, figs 26, 27 (*Mnesarchaea*). Hudson, 1928, p. 367 [partim], but not pl. L, fig. 2 (which shows *M. hudsoni*).

Diagnosis (Figs 3, 4, 138, 139). A small dark brown northern South Island species, with scattered ochreous-yellow scales, **forewing length not exceeding 3.5 mm**; male genitalia with a pair of heavily melanised **outwardly**

bent periphallid arms, arising from the pseudoteguminal plate (the tips of which are usually visible in dried specimens) in addition to a pair of largely unmelanised phallomeres. Similar species: *hudsoni*, *fallax*.

Male (Figs 3, 138). Head vestiture including palps ochreous to ochreous-brown, dark brown on postmentum. Antennae 0.56–0.63 of forewing with 31–34 flagellomeres; scales usually yellow-ochreous sometimes darker ochreous-brown, darker toward tip. Thorax: dorsal vestiture brown with scattered ochreous scales, tegulae brown and ochreous, prosternum ochreous to dark brown. Forewing 3.1–3.5 mm, length/width ratio 3.9; uniformly dark brown with purple-golden reflections and a diffused spangling of ochreous-yellow scales over most of the wing concentrated in three areas- a patch at tornus, and two subapical patches at 4/5 one on costa and the other on termen. Fringes dark brown with ochreous patches on tornus at 1/2 and on costa and termen at 4/5; also scattered long ochreous scales along termen, interspersed with shorter brown scales. Hindwing uniform brown with purple-golden reflections, slightly paler than forewings. When at rest, exposed legs dark brown scaled, with narrow ochreous bands at distal end of joints, meso- and meta-femora and undersurface ochreous, spurs dark brown but spines ochreous. Epiphysis vestigial or absent. Abdomen dark brown above with some pale whitish-brown scales ventrally.

Female (Figs 4, 139). Antennae 0.47 of forewing with 29 flagellomeres. Forewing 3.2 mm, with ochreous scales more dense than in male giving a much paler overall appearance (Fig. 4).

Male genitalia (Figs 66, 80) (6 preparations). Dominated by the pair of massive lateral periphallid arms arising from the pseudoteguminal plates and articulating in the dorsal mid-line, their apices slightly asymmetrical, with pointed tips turned outwards. Below these, a pair of much smaller subanal periphallid arms arise from the base of the anal cone, slightly shorter than pseudoteguminal arms, narrower and largely unmelanised, tapering, with apices clothed in microtrichia. Roof of subgenital crypt supported by an H-shaped sclerotisation of the pseudoteguminal plate. Valva with broad articulation, club-like in side view with a narrow neck and rounded head but broad from below due to a wide keel along the dorsal margin; a shelf-like flange projecting below the upper arm on ventral side; arm and adjacent edge of lower valva darkly melanised; inner aspect with two groups of setae along the keel; valvae separated in the mid-line by a wide, unmelanised crenulated zone bearing a patch of thin setae on each side, possibly representing the juxta. Vinculum broadly shield-shaped with a convex anterior margin. (Genitalia slide G430, NZAC, Picton, GWG. NZAC.)

Female genitalia (Fig. 95) (1 preparation). Dorsal lobes 0.1 of total dorsal plate length; the dorsal plate flask-shaped in ventral view with convex sides giving it a maximum width near point of articulation of 0.6 of its length. Subgenital plate narrower than subdorsal plate and reaching to 0.8 of its length; maximum width 0.6 of length; anterior margin straight with simple lateral hinges; posterior apex broad, bilobed with a very shallow median notch; three patches of microtrichia, one along posterior half in the central area, the others on each side near the hinge. Antrum extending about as far anteriorly from the subgenital plate hinge-line as it does posteriorly; with a longitudinal pocket along each side in the vicinity of the hinge and a median melanised flange, tapering anteriorly toward the ductus; roof with close-set spinules, predominantly comb-like medially with spines laterally; floor with random clusters of minute spines. Ductus without spinules. (Genitalia G420, in glycerine, temporary mount, Picton, GGNZ).

Larva. 6 mm. Young larvae bright green becoming brownish-green towards maturity. Indistinguishable from *hudsoni*.

Type data. Holotype male, Goulard Downs, 7 Feb 1922, A. Philpott. NZAC.

Material examined. Holotype plus 52 non-type examples (50 males, 2 females and 4 larvae, BMNH, NZAC, GGNZ, MONZ). See Appendix 1 for list of collection localities. .

Distribution. SD, NN.

Flight Season. 19 December to 18 February.

Remarks. This species ranges from sea-level up to 1000m, occurring in deep gullies and ravines in forests where light penetration is often poor. It also occurs along stream banks where swards of dense green periphyton are present and is often associated with filmy ferns and blechnaceous ferns. Although its distribution overlaps with *fallax*, *acuta* and *hamadelpha*, its later flight season ensures that it is not normally found with other mnesarchaeid species.

The early literature (Philpott 1922a, Hudson 1928) suggests that *fusca* occurs in the North Island at Wellington. It is unfortunate that Philpott (1927b) did not examine the genitalia of Hudson's Wellington specimens

since he would have realised that although so similar in external appearance, the North Island species is quite distinct. Thus the specimen figured by Hudson (1928, pl. L. fig.2) as *fusca* from Wilton's Bush (Otari Native Plant Reserve) is surely *hudsoni*. Apart from the collection locality, the only positive way to identify these two species is by genital dissection. Their larvae cannot be discriminated with our present limited knowledge of larval characters.

***Mnesarchaea hudsoni* Gibbs, new species**

Figs 5, 6, 31, 48, 67, 81, 96, 140; Map 3.

fusca [partim], Hudson 1928, p. 367, pl. L, fig. 2 (*Mnesarchaea*) (misidentification).

Diagnosis (Figs 5, 6, 140). A dark brown North Island species, with scattered ochreous scales; forewing length >3.4 mm, antennae bright ochreous yellow; male genitalia with a **pair of long, melanised, sharply pointed phallomeres, slightly inturned at apex and projecting posteriorly well beyond two other pairs of shorter phallomeres** (usually visible in dried specimens) (Fig 81). Similar species: *fusca*, *fallax*.

Male (Figs 5, 140). Head vestiture pale ochreous-brown, dark brown on postmentum, palps pale ochreous-yellow with some brown scales; antennae 0.60–0.65 of forewing with 34–35 flagellomeres in male; scape dark brown, flagellar scales bright ochreous-yellow, slightly browner towards tip. Thorax dorsal vestiture ochreous-brown to brown, tegulae dark brown, prosternum dark brown. Forewing 3.4–4.2 mm, length/width ratio 3.7; uniformly dark brown with purple-golden reflections and a diffused spangling of ochreous scales over most of the wing, concentrated into poorly defined patches on tornus at 1/2 and on costa at 4/5. Fringes dark brown with ochreous patches at tornus and on costa and termen at 4/5, also along most of the termen from Rs4 to M3 where the shorter scales are brown but longer ones ochreous. Hindwings uniform dark brown with purple-golden reflections, same tone as forewings. Legs mostly dark brown with areas of paler brown scales where not exposed (on meso- and meta-femur), a narrow distal band of ochreous on tibiae and each tarsal joint, tarsi ochreous beneath; spurs brown above, ochreous below; spines mostly ochreous. Epiphysis vestigial (Fig. 48). Abdomen dark brown above with pale brown scales below; genital fringes dark brown.

Female (Fig 6). Antennae 0.48 of forewing with 31–32 flagellomeres. Forewing 4.0 mm, with ochreous scales more dense than in male giving a paler overall appearance.

Male genitalia (Figs 67, 81) (8 preparations). Pseudoteguminal plates symmetrical, each consisting of a transverse bar across the roof of the genital capsule, giving rise to two pairs of symmetrical, darkly melanised lateral periphallalic arms of about the same length as the valva, one inner pair and one outer; each arm with an out-turned tip, bluntly pointed. Additionally, a pair of subanal periphallalic arms, very long and straight, projecting well beyond other genital elements—narrow, tapering, with fine tips, lacking texture or microtrichia. Roof of subgenital crypt supported by an H-shaped pseudoteguminal sclerotisation. Valva broad-based, slightly expanded distally; outer face convex but inner face with a longitudinal keel; upper arm tapering with a pointed apex, below it a rounded shelf-like lobe projects on ventral side; entire upper arm and crescentic band below it strongly melanised; a group of 30–40 thickened curved setae toward base of inner keel. Vinculum broadly shield-shaped with a convex anterior margin. (Genitalia slide G458, Wilton's Bush, Wellington, GWG. NZAC.)

Female genitalia (Fig. 96) (4 preparations). Dorsal lobes 0.14 of total dorsal plate length; the dorsal plate almost straight-sided in ventral view, elongate triangular with a maximum width near point of articulation of 0.63 of its length. Subgenital plate reaching to 0.77 of length of dorsal plate; narrow and only slightly tapering; its maximum width at hinge 0.73 of its length; anterior margin straight with simple lateral hinges; posterior apex broad, wider than base of dorsal lobes and with very shallow median notch or lacking notch altogether; densely covered with microtrichia over distal half leaving extreme margins smooth; a few microtrichia on lateral edge at hinge. Antrum extending about as far anteriorly from the subgenital plate hinge point as it does posteriorly; partially divided longitudinally into two lateral pockets in vicinity of hinge, and with a longitudinal ridge in roof of anterior portion; a very complex array of spinules on both roof and floor, mainly comb-like but with needle-like spines in "throat" region. Ductus without spinules. (Genitalia G454, glycerine in minivial, Otaki Forks, GGNZ).

Larva. 6 mm. Cuticle in life unicolorous, bright green in young larvae, becoming brownish-green towards maturity; microtrichia unmelanised, imparting a whitish pubescence at x50 in life. Head capsule and pinnacula greenish-brown, labrum and mandibles yellow-brown, trunk setae black. Chaetotaxy as for *paracosma*. Mature larva with about 20 macrocrochets on prolegs and with a head capsule width of 0.47 mm.

Type data. Holotype male: Wilton's Bush (= Otari Plant Reserve), WN, 7–9 Mar 1922. G.V. Hudson, MONZ. Paratypes: 6 males, 1 female as follows: 1 female, Otari Plant Reserve, WN, 6 Mar 2010, G.W. Gibbs (NZAC); 1 male, Otari Plant Reserve, WN, 2 Mar 1979, G.W. Gibbs (genitalia slide G458) (NZAC); 1 male, Gollans Valley, East Harbour Regional Park, WN, 4 Mar 1979, G.W. Gibbs (NZAC); 1 male, Otaki Forks, Tararua Forest Park, WN, 5 Apr 1980, (Fig. 5), G.W. Gibbs (NZAC); 1 male, Otaki Forks, WN, 5 Apr 1980, MONZ; 1 male, Otaki Forks, 16 Mar 2010, MONZ.

Material examined. Type and 100 non-type examples (95 males, 5 females and 19 larvae, BMNH, NZAC, MONZ, CMNZ). See Appendix 1 for list of collection localities.

Distribution. AK, CL, BP, TO, GB, HB, WA, WN.

Flight Season. 4 February to 5 April.

Remarks. This species frequents deep forest ravines and well shaded banks alongside tracks or streams from sea-level to about 800 m. Larvae spend the winter in the 1st or 2nd instar until about the end of October, at which time they may co-occur with mature larvae of *Mnesarchella fusilella*, *acuta* or other *Mnesarchella* species. The main larval growth takes place in summer, thus explaining perhaps why this species (and *fusca*) are generally more confined to wetter, well shaded sites than other mnesarchaeids.

The understandable confusion of this species with *fusca* has been discussed above. Males can usually be distinguished without dissection by looking for the straight, pointed tips of the projecting phallomeres which are normally evident in the centre of the genital area of dried specimens.

Etymology. Named in honour of G.V. Hudson who discovered this species at one of his favourite collecting localities and contributed so much to our knowledge of New Zealand Lepidoptera.

***Mnesarchaea paracosma* Meyrick, 1885**

Figs 7, 8, 25, 27, 33, 34, 36, 50, 51, 52, 68, 82, 97, 115, 116, 141, 142; Map 4.

paracosma Meyrick, 1885, p. 591 (*Mnesarchaea*); Meyrick 1886, p. 180 (*Mnesarchaea*). Hudson 1928, p. 366, pl. XXXIX fig. 26 (*Mnesarchaea*). Philpott 1927b, p. 712, fig. 25 (*Mnesarchaea*).

Diagnosis (Figs 7, 8, 141). An ochreous-brown species with pale ochreous-yellow antennae and a diffuse maculation of brown, white and yellowish scales. Male genitalia with a complex array of **five distinctly asymmetrical posteriorly-directed processes** (Fig. 82).

Male (Figs 7, 141). Head vestiture pale ochreous dorsally but pale brown ventrally. Antennae 0.55–0.65 of forewing with 32–36 flagellomeres; scape pale brown, pedicel and flagellar scales pale ochreous-yellow throughout. Dorsal vestiture of thorax including tegulae, pale ochreous-brown; sides almost white. Forewing 3.3–4.2 mm, length/width ratio 4.0; ground colour pale brown with golden reflections; basal 1/2 pale brown toward margins with central area ochreous-yellow along cubital fold, spangled with white scales; a conspicuous oblique white fascia from costa at 2/5 to centre of wing at 1/2; apical area of mixed white, dark brown and ochreous-yellow scales with two white patches at 4/5, one on costa and one on termen; apical area predominately dark brown. Fringes brown with white patches on tornus at 1/2 (CuP) and on costa at 4/5 and termen at M2 and between M1 and Rs4. Hindwings uniform pale brown with strong purple-golden reflections, overall a slightly darker tone than forewing. Legs pale ochreous on femora, exposed surfaces dark brown with narrow off-white bands at distal end of each joint, tarsi ochreous beneath, spurs and spines pale ochreous. **Epiphysis absent**. Abdomen silvery brown above, very pale, almost white below.

Female (Figs 8, 142). Antenna 0.52–0.53 of forewing with 28–30 flagellomeres. Forewing 3.3–3.8 mm; overall distinctly paler than male, forewing maculation similar but with a wide pale ochreous-white area along dorsum to just beyond 1/2; white patches at 4/5 joined across wing to form a transverse fascia. Hindwing uniform pale grey-brown.

Male genitalia (Figs 68, 82) (4 preparations). Pseudoteguminal plate with 5 conspicuous, asymmetrical, long pointed posterior processes (periphallic arms); two distinct 'T'-shaped sclerotised components of each plate lie across the roof of the genital capsule and curve around its lateral margins, each giving rise to a long lateral periphallic arm. The left hand plate is the larger, extending to the mid-dorsal line where it gives rise to the longest (0.57 mm) arm, sharply-pointed and almost straight, but curving gently downwards and to the left near its distal extremity. The smaller right-hand plate gives rise to a slightly shorter arm, strongly kinked to the right. Slightly to the right of the dorsal mid-line and below the preceding arms, is a third lateral periphallic arm, darkly melanised,

tapering and curving to the left, carrying the anal cone with it. Yet another pair of long, parallel, symmetrical subanal periphallid arms, distinguished by their microtrichiated apices, extend posteriorly either side of the mid-line. Roof of subgenital crypt supported by an H-shaped pseudoteguminal sclerotisation. Juxta not discernable. Valva broad-based, slightly tapering; smoothly convex on both inner and outer faces; the upper arm tapering to a pointed apex partly overlapped by distal flange of the lower valva, inner surface with 30–50 thickened setae. Vinculum transverse, with a strongly concave anterior margin and a pair of blunt posterior processes projecting free beneath the valvae. (Genitalia slide G437, Mt Alfred Track, L. Wakatipu, GWG. NZAC.)

Female genitalia (Fig. 97) (1 preparation). Dorsal lobes 0.1 of total dorsal plate length; the dorsal plate broadly flask-shaped in ventral view with markedly convex sides giving a maximum width midway of 0.5 of its length. Subgenital plate reaching to 0.8 of dorsal plate length; more or less parallel sided with a maximum width of 0.4 of its length; shoe-horn shaped with a median keel at the anterior end; hinge line complex, consisting of a triangular pocket on each side of the ventral mid-line, open to the posterior across their bases and with the dorsal and subgenital plates fused together along their outer sides; posterior apex broad, wider than the base of the dorsal lobes and with a very shallow median notch; a small area of microtrichia near the apex. Antrum extends forward of the hinge for slightly more than half of the sternite length; with a longitudinal pocket along each side; roof with two types of spinules: comb-like in centre, needle-like along margins with the latter predominating in the "throat" region of the hinge; floor spinules minute, in hexagonal pattern. Ductus with small spinules developed along one side only in distal half. (Genitalia G433, glycerine minivial, Takitimu Range, GGNZ.)

Larva (Fig. 25). 6 mm. Cuticle translucent leaf-green in life, unicolourous, with melanised microtrichia conspicuous at x100. Head capsule yellow-brown, darker to almost black around the postociput; pinnacula and thoracic legs brown; setae black. Prolegs translucent with 23–29 macrocrochets. Chaetotaxy (Fig. 18): Prothorax with L3 well clear of shield margin and closer to spiracle; abdominal segments 1–6 with 4 SV setae. Mature head capsule width 0.50 mm.

Type data. Lectotype ♂ designated by Dugdale (1988, p.55) 7/5 from type series of 5 males from Lake Wakatipu (OL), 15 Dec.1882 and 1 male from Invercargill (SL), 13 Dec 1882. E. Meyrick. BMNH. Meyrick's diary confirms his visits to both localities on those dates.

Material examined. Type series and 106 non-type examples (102 males, 4 females and 18 larvae, BMNH, NZAC, CMNZ, LUNZ, MONZ, GGNZ, BPNZ). See Appendix 1 for list of collection localities.

Distribution. KA, MC, SC, MK, OL, CO, DN, FD, SL.

Flight Season. 29 October to 18 February.

Remarks. The known habitats are extremely variable, ranging from open mossy beech or podocarp forests to tussocklands or shrublands. Since the larvae require moist periphyton, adults are unlikely to be found away from seepage areas unless the locality receives very regular rainfall. Altitude records also range widely from near sea-level to 1200 m. The extensive flight season is partly a reflection of its wide climatic range, but in his former Dunedin garden, Brian Patrick found the flight period of this species to extend over a period of 8 weeks (pers. comm.). Although normally diurnal, this species has been taken in a light trap (B. Patrick pers. comm.).

Structurally the most complex of the *Mnesarchaea* species, exhibiting extraordinary male genitalic developments akin to some of the Prototheoridae (Davis 1996) and *Paratheora* (Simonsen & Kristensen 2017) but with pronounced asymmetry. Further collecting in the eastern and southern South Island will undoubtedly provide many new localities for this small, easily overlooked species.

Genus *Mnesarchella* Gibbs, new genus

Figs 9–19, 20–24, 26, 28–30, 32, 35, 37, 39, 40–49, 53–55, 57, 62–64, 69–78, 83–92, 98–114, 117–133, 143–156.

Maps 5–14.

Type species: *Mnesarchaea acuta* Philpott, 1929, here designated.

Note. The ten species in this genus are markedly distinct from those of *Mnesarchaea* in every respect. Morphological discrimination between species is relatively straightforward but for the sake of rapid, and consequently superficial, identification they are presented in two species groups – an *acuta*-group of seven look-alike species with near identical maculation and a *fusilella*-group of three species that can be distinguished by colour maculation alone. Phylogenetically, the latter three comprise a monophyletic group embedded in the 10-species *Mnesarchella* clade.

Diagnosis. Head vestiture white or ochreous with a dark brown lateral streak incorporating the eye.

This streak is comprised of dark brown scales on genal area, the brown eye itself and the melanised portion of the head capsule between the eye and the antennal socket which is usually devoid of scales. In living insects at rest the eye streak is aligned with the dark brown costal wing streak as shown in the colour figures. Flagellar segments of **antennae with unbranched sensilla trichodea** (Fig. 32). **Thorax dorsal vestiture white or ochreous.** Forewings with extensive whitish basal area within the cell and a strong dark brown costal streak (exception *dugdalei*). Forewing venation (Fig. 57) with M1 arising from the stalk of Rs3+4 (exceptions *fusilella*, *loxoscia*). Abdomen silvery greyish-brown, paler beneath, with a male genital fringe of long whitish parallel-sided scales arising from the outer surface of the valvae.

Larva (Figs 24, 109). Head capsule orange-brown, darker around postociput; trunk unicolorous, in life varying from pale ochraceous-brown through olive-brown to dark slaty-grey but never green; pinacula and leg sclerites dark-brown; trunk densely clothed with melanised microtrichia (except in first instar), clearly visible in light microscope at x100. Trunk chaetotaxy (Figs 113, 114): prothorax with L3 very close to lateral margin of shield or incorporated into it, spiracular pinaculum elongate with pointed apex (Fig. 130); metathorax with SD1 closer to SD2 than to L3; abdominal segments 1–6 with L2 vertically below spiracle and with 3 SV setae. Mature larvae with 14–19 macrocrochets in a biserial circle (Figs 132, 133).

Male genitalia (Figs 62–64, 83–92). Vinculum wider than long, somewhat crescent-shaped, convex anteriorly, sometimes also produced posteromedially; an internal longitudinal costa may or may not be present, its development varying even within species. T10 paired lobes rounded, densely clothed with microtrichia and setae. Periphallitic arms undeveloped (exception *falcata*). Posterior (eversible) part of male duct usually with two clusters of cornuti arising from a common lightly-sclerotised base; in *dugdalei* forming prominent processes, entirely absent in *fusilella* and *philpotti*. Roof of subgenital crypt with prominent, very darkly melanised trulleum mounds in 6 species, bluntly granular or spinose. These trulleum lobes, opposed by the pecten bristles of the valvae, almost certainly play a grasping role during copulation. An oval pit is frequently present in the midline in the vicinity of the trulleum melanisations (exceptions *acuta*, *ngahuru*, *stellae*, *vulcanica*) leading into a cavity where the cellular structure indicates a possible glandular function. Valva morphology similar throughout group—each bilobed with a slender dorsal arm and shovel-like ventral lobe bearing numerous strong recurved setae on inner surface which, in 8 species, are organised into a dense comb-like row or patch (the 'pecten'). Characteristics of the distal end of the dorsal arm may be taxonomically useful.

Female genitalia (Figs 98–108). Posterodorsal lobes (Fig. 99) rounded and separated by a broad U-shaped notch, the lobes recessed ventrally to accept curvature of ovum, lightly melanised, setose and densely covered with microtrichia. These lobes consistent throughout the group and of no taxonomic value. Subgenital plate broad and scoop-like, tapering from its widest point at the anterior hinge to a relatively broad rounded posterior apex, sometimes with a shallow median notch; exposed ventral surface sparsely clothed with long piliform scales anteriorly, giving way to true setae towards posterior apex, smooth or partly set with fields of microtrichia, which can provide useful taxonomic characters. Antrum region of ductus largely thin and membranous but with a conspicuous melanised V-sclerite supporting the sides beneath the ovipore (exception *falcata* where V-sclerite absent). Corpus bursae as long as abdomen, parallel-sided (exception *falcata* with oval bursa). Spermatheca on a long duct which has 2–3 spiral turns (Fig. 98).

The *acuta*-group of species

Confusion between wing patterns of *hamadelpha* and *acuta* led to early identification problems for Philpott (1924, 1927b) and Hudson (1928, 1939) until Philpott (1929) resolved the issue through correspondence with Meyrick. The existence of a further five *Mnesarchella* species which also share this maculation had escaped attention until now despite their occurrence in collections since the 1920s. The diagnostic colouration of these seven species is described here to avoid repetition in the species descriptions.

The shared forewing maculation is shown in Figs 9–15 and 143–150; it is a complex pattern of white, dark-brown and pale ochreous-brown scales, the latter with strong golden reflections. A diagnostic **dark-brown crescent-shaped costal streak, its inner edge along the radial vein but curving inward around the end of the cell from about 2/5 to terminate in the centre of the wing.** Remaining basal area of wing intensely white or

ochreous-white in the cell with a variable suffusion of pale golden-brown scales toward the dorsum and a small dark-brown oblique anal fascia. The more-or-less triangular apical half of the wing beyond the costal streak is of pale golden-brown ground colour with a white 'costal patch' on the costa beyond the costal streak and a confusing array of white, golden-brown, dark-brown and black scales which make up a complex mini-fascia of little value for diagnosis. Fringes pale ochreous-brown with some black and white scales at apex, zones of white fringe scales occur at Rs1+2, M1 and CuP. Hindwings and fringes brownish-grey with weak purple reflections, some specimens with a distinct darkening at apex.

Male genitalia of the seven *acuta*-group species differ from each other to a greater extent than these differ from the three *fusilella*-group species—a not unexpected situation when viewed in terms of the status of the entire genus as a monophyly. A diagnostic autapomorphy for the *acuta*-group species is the cornuti of which the base plate bears **multiple acutely-pointed spines** (however, *falcata* and *philpotti* lack cornuti, *falcata* instead with a pair of large, conspicuous peripheral arms.) For comparison, cornuti of the *fusilella*-group species are large with a single or double spine (e.g. compare Figs 83 and 92). The relative lengths of dorsal vs ventral valva arms are cited for *fusilella*-group diagnosis but relate to a feature that can be difficult to assess. It is best seen in the series of Figs 69–78 in which the ventral view of genitalia is shown in situ. The **dorsal valva arm of *acuta*-group species is approximately the same length or distinctly shorter than the ventral arm.**

Note. Rapid diagnostic characters are given only for males because females are rarely taken and, in some instances, can be difficult to discriminate without association with known males, specific locality information, or detailed structural examination.

***Mnesarchella acuta* (Philpott, 1929) new combination**

Figs 9, 20–22, 24, 26, 28–30, 32, 35, 37, 41–45, 48, 49, 53–55, 57, 62–64, 69, 83, 99, 109–114, 117–123, 127, 143, 144; Map 5.

acuta Philpott, 1929, p. 304 (*Mnesarchaea*). Hudson 1939, p. 470 (*Mnesarchaea*).

hamadelpha sensu Philpott 1927b, p. 711, Figs 1, 2, 5, 6, 23 (*Mnesarchaea*) (misidentification). Hudson 1928, p. 367, pl. XXXIX, fig. 24 (*Mnesarchaea*) (misidentification).

Diagnosis (Figs 9, 143, 144). An *acuta*-group species in which the **white areas are intensely white**. The distal end of the **dorsal valve arm carries a finger-like extension**; pecten bristles are grouped into a **dense patch** in the centre of the valve lobe (not a comb), well clear of the posterior edge. Similar species: all those in *acuta*-group.

Male (Fig 143). Head vestiture intense white or very occasionally with an ochreous tinge. Antennae 0.55–0.65 of forewing with 34–36 flagellomeres. Thorax dorsal vestiture white, very rarely tinged yellow-brown. Forewing 4.2–5.2 mm, with white basal area usually not suffused with pale ochreous; median costal patch slightly off-white. Epiphysis present, moderate (Fig 48).

Female (Figs 9, 144). Antennae 0.4–0.5 of forewing with 29–31 flagellomeres. Forewing 4.1–4.8 mm; maculation as for male but whole apical area more whitish. Hindwing also paler, suffused with some pale-ochreous scales towards apex with a patch of dark-brown scales at apex.

Male genitalia (Figs 62–64, 69, 83) (56 preparations). **Trulleum melanisation present, in form of two bluntly spinose mounds separated by a deep narrow posterior notch**, each mound with its lateral dimension greater than its longitudinal dimension (Fig. 43). Valva essentially unmelanised, with dorsal arm apex drawn out into a **finger-like process** bearing 1 or 2 very fine setae and with 25–30 longer setae along inner face of the arm; ventral lobe about as long as dorsal arm with its posterior angle acute; **pecten present, a very dense, roughly triangular patch of 80–100 stout pointed bristles across centre of lobe** with a further 30 or more scattered supernumerary setae between pecten and apex; outer edge with series of recurved setae. Up to about 14 simple conical cornuti of varying length from small to moderate arising from two oval base-plates. (Genitalia slide G217, Nelson Reservoir camp, GWG. NZAC.)

Female genitalia (Fig. 99) (5 preparations). Subgenital plate smooth except for a small field of microtrichia along each postero-lateral margin; roof of antrum with a narrow transverse melanised band at widest point of V-sclerite just anterior to the hinge line, interrupted in middle and bearing numerous triangular tooth-like scutes; a hexagonal pattern discernible in centre, between the two lateral V-sclerite arms. Ductus with comb-like spinules throughout. (Genitalia G214, Welcome Flats, Copeland V, minivial in glycerine, GGNZ.)

Larva (Figs 24, 109). Head capsule orange-brown; trunk cuticle unicolourous olive-brown in life with dark brown legs and pinacula, setae black. For chaetotaxy see *acuta*-group description. The larva reaches a maximum of 10 mm total length at maturity. Head width measurements (in mm) in the four larval instars are: 0.23 (0.22–0.25); 0.34 (0.32–0.35); 0.47 (0.45–0.50); 0.70 mm (0.65–0.73).

Type data. The presumed type material is in NZAC, but is not labelled as such: there are 7 specimens in the Philpott Collection taken at Arthurs Pass (NC) on 9 and 16 Jan. 1920. In the original description, Philpott does not give a type locality but mentions a holotype male, an allotype female and a series of paratypes in the Cawthron Institute. Three male genitalic slides prepared by Philpott (NZAC) lack any collection data, but are presumed to be from this series, all but one of which lack abdomens. Genitalia slide H281 (I.F.B. Common, ANIC) represents one specimen from this type series. Dugdale (1988) notes that the specimens were possibly collected by R.J. Tillyard. Because of the lack of labelling, the presumed type series is effectively syntypic, in spite of Philpott's mention of a holotype (Z.-Q. Zhang pers. comm.), but based on the locality, the external appearance of the specimens and the available genitalia slides, there is no ambiguity about the identity of these specimens; therefore there is no need to designate a lectotype. There is no clear evidence that the holotype has been lost or destroyed, so a neotype designation is also inappropriate.

Material examined. Presumed type series plus numerous non-type examples (males, females, plus 72 larvae). BMNH, NZAC, AMNZ, CUNZ, GGNZ.). See Appendix 1 for list of collection localities.

Distribution. RI, WN / SD, NN, BR, WD, KA, NC.

Flight season. 7 October to 26 January.

Remarks. A very common species compared with the other two *acuta*-group species within its distribution area (*hamadelpha* and *stellae*). Known from a variety of habitats in forest, on river banks and in low shrub and herb communities provided they are moist and not subject to all-day sunshine. Its altitude range is from sea level to 900 m, in dense lowland rain forest or open mossy beech forest. Occasionally it co-occurs with *fusilella* or *loxoscia* but it is not known to co-occur with other *acuta*-group species although it may be found near to them. Although this revision cites the northern distribution limit as Pohangina Gorge, it should be noted that the Hudson collection Register includes a specimen of '*acuta*' labeled '267n' from the Ohukune Mountain Track (end Jan 1912). Genitalia preps (G525, G526) showed it to be conspecific with another GVH specimen (267a) from Wellington. The most plausible explanation is that the finding of *acuta* on Ruapehu must remain as a possibility. It is diurnal and has not been taken at light. Males fly frequently, especially in cool, filtered sunshine after rain, but females are sedentary and seldom taken.

The life cycle is univoltine with a flight season of up to 7 weeks at any one locality. Larvae develop slowly through their first two instars, reaching the third instar by about the end of April and the final instar by July with pupation in October–November.

The concept of this taxon had a very hesitant beginning. Although collected very early, first by E. Meyrick in 1886 at Nelson (NN) and then by G.V.Hudson in 1896 at Khandallah (WN), these specimens were assumed to be *hamadelpha* Meyrick, 1888. It continued to be collected and referred to *hamadelpha* by New Zealand lepidopterists until Philpott's genitalic studies (1927b) revealed the two distinct taxa and finally resolved the confusion (Philpott 1929). The "*acuta*-type" maculation continued to mask the true identity of *ngahuru*, *philpotti*, and *vulcanica*, all of which had been collected between 1919 and 1930 by M.N. Watt, C.E. Clarke and A. Philpott respectively, but attributed to *acuta*.

***Mnesarchella falcata* Gibbs, new species**

Figs 10, 40, 70, 84, 100, 145; Map 6.

Diagnosis (Figs 10, 145). An *acuta*-group species in which the male genitalia have a unique pair of **short sclerotised periphallallic arms** with upturned pointed tips, protruding from below the anus. Similar species: all *acuta*-group.

Male (Figs 10, 145). Head vestiture white to pale ochreous-white; antennae 0.65–0.70 of forewing with 35–39 flagellomeres. Thorax dorsal vestiture brownish-white. Forewing 4.1–5.0 mm; basal area white to ochreous-white blending to pale brown along cubital fold; oblique dark-brown anal fascia extends from margin to tip of costal streak; median costal patch pale ochreous-white; a patch of intense white scales in centre of apical area on fork of R and M1; apex with 2 layers of dark-brown fringe scales. Legs distinctive due to absence of ochreous

scales on ventral side of hind tarsi except apically, i.e. brown scales encircle the tarsus although ochreous distal bands persist. Epiphysis present, long. Abdomen almost as dark beneath as above.

Female. Antennae 0.44–0.50 of forewing with 30–32 flagellomeres; flagellar scales brown. Forewing 4.0–4.5 mm. Legs with ochreous scales ventrally.

Male genitalia (Figs 40, 70, 84) (11 preparations). Dorsal recess with a pair of thick sclerotised periphallallic arms below the anal membrane, each about the same length as a dorsal lobe, tapering slightly with an upturned tip. Trulleum only diffusely melanised, lacking discrete sclerotised mounds and with a small glandular area in the mid-line. Valva essentially unmelanised, with distal apex of dorsal arm slightly expanded, rounded and bearing an array of about 12 long thin curved setae with a further 15–20 similar setae along its inner face; ventral lobe as long as arm, with posterior angle acute; pecten present, a single row of 12–16 heavy blunt bristles with strong elliptical bases, situated transversely across the lobe and towards its base: about 70 short setae between pecten and apex. Cornuti absent. (Genitalia slide G522, Ohakune, GWG, NZAC.)

Female genitalia (Fig 100) (4 preparations). Unique, the most distinctive of *acuta*-group species. Subgenital plate with a keeled posterior apex, the keel bearing a row of about 5 median setae near the apex; dense microtrichia present over posterior half. V-sclerite absent but lateral margins of antrum lightly melanised. Roof of antrum essentially without spinules apart from some minute vestiges near the anterior end. Ductus lacking spinules throughout. Bursa small and oval, not extending beyond segment A6. (Genitalia G317, Waitanguru, GWG, minivial in glycerine, GGNZ.)

Larva. Although some extremely darkly pigmented *acuta*-group larvae are known from Erua in the Tongariro N.P., a site where *falcata* has occurred commonly, they cannot be assigned to this species with any certainty due to the co-occurrence of both *ngahuru* and *loxoscia* at this site.

Type data. Holotype: male labelled "New Zealand TO, Ranger Station, Mangawhero Stm Ohakune 650m, 7 Dec 1983, G.W. Gibbs" (white card), "HOLOTYPE *Mnesarchella falcata* Gibbs NZAC" (red card), Fig 145 (NZAC).

Paratypes: 1 female, 4 males, as follows: 1 female (unspread), Ohakune Mountain Road at Mangawhero Stream bridge, 900m 7 Dec 1983. (NZAC); 1 male, Ranger Station, Ohakune, 650m, 7 Dec 1983 (genitalia slide G522, NZAC); 2 males, Mangawhero Stream Bridge, 900m, 7 Dec 1983 (MONZ).

Material examined. Type series plus 28 non-type examples (25 males, 3 females). See Appendix 1 for list of collection localities.

Distribution. WO, TO, HB, RI.

Flight season. 22 November to 31 December.

Remarks. A distinctive mid to upper altitude forest species with a known range between 650 and 1100 m. Its habitats are mossy montane forests of rimu, red or silver beech and cedar (*Libocedrus bidwillii*) with good light penetration. Where *falcata* co-occurs with *vulcanica* (e.g. Tongariro N.P., Kaimanawa F.P.), it appears at a slightly lower altitude. It has been found with *dugdalei* in November to December (at L. Rotopounamu, Tongariro N.P.; Coromandel Range; Whanganui N.P.) and with *loxoscia* in late December (Te Iringa Hut Track, Kaimanawa F.P.).

External features are not reliable for distinguishing this species from *vulcanica*.

Etymology. Named with reference to the sickle-shaped periphallallic arms in the male genitalia which discriminate this species from all other *Mnesarchella* species.

***Mnesarchella hamadelpha* (Meyrick, 1888) new combination**

Figs 11, 46, 47, 71, 85, 101, 146; Map 7.

hamadelpha Meyrick 1888, p. 91 (*Mnesarchaea*); Hudson 1939, p. 470, pl. LXI, fig. 8 (*Mnesarchaea*).

similis Philpott 1924, p. 667, fig. 4 (*Mnesarchaea*); Philpott 1927b, p. 711, figs 4, 7, 22. Synonymised by Hudson (1928, p. 367).

Diagnosis: (Figs 11, 85, 146). An *acuta*-group species with posterior margin of the pseudoteguminal plate developed into a pair of unique **spinose finger-like trulleum** projections, separated by a broad U-shaped emargination. Similar species: all other *acuta*-group.

Male. (Figs 11, 146). Head vestiture ochreous-white; antennae 0.54–0.66 of forewing with 34–36 flagellomeres. Thorax dorsal vestiture pale ochreous-brown. Forewing 4.5–5.1 mm; basal area in cell ochreous-white, grading into pale ochreous-brown along dorsum and with the oblique dark-brown anal fascia quite diffuse—

reaching neither to subcostal streak nor anal margin; median costal patch ochreous-white with a patch of white scales on distal side of the costal streak apex. Hindwing sometimes with a dark spot at apex. Epiphysis absent.

Female. Antennae 0.45 of forewing with 28 flagellomeres. Forewing 3.9–4.2 mm; similar to male but whitish scales predominate over pale brown along dorsum and in subapical section.

Male genitalia (Figs 71, 85) (30 preparations). Trulleum melanisation bluntly spinose, restricted to apex and inner margins of a broad U-shaped posterior emargination of the pseudoteguminal plate; conspicuous oval glandular pit present in front of the emargination. Valva essentially unmelanised; dorsal arm slightly curved, distal end truncate with 2–3 fine setae and with 15–20 long thin setae along inner face; ventral lobe as long as arms, its posterior margin markedly concave, resulting in an acute posterior angle; pecten present in centre, a single transverse row of 8–22 blunt bristles, with a diffuse patch of 20–30 slightly curved pointed setae between pecten and posterior angle, some recurved setae along outer edge. Cornuti present, up to about 7 pairs of simple moderate-sized conical spines together with smaller supernumerary spines, on two separate base-plates. (Genitalia slide G274, Karamea Bluff, 6 Dec 1986, GGNZ.)

Female genitalia (Fig. 101) (3 preparations). Subgenital plate with microtrichia covering entire posterior half except for a narrow marginal strip. Roof of antrum lacking any melanised band but with a large triangular patch of spinules in its anterior half, comprising single spines, comb-edged spines and teeth; hexagonal pattern absent. Ductus with dense comb-like spinules towards anterior end and sparse simple spinules posteriorly. (Genitalia G.270, Mt Dundas, Tararua Range, glycerine in minivial, GGNZ.)

Larva unknown.

Type data. Lectotype male (designated by Dugdale 1988, p. 55), Mt Arthur (NN) 19 Jan 1886, E. Meyrick, BMNH. Genitalia slide no 23421, BMNH.

Holotype male of *similis*, Cobb Valley (NN), 9 Dec. 1922, A. Philpott, NZAC. Genitalia slide, Philpott Collection, NZAC, bears the annotation “This may be HT genitalia, as only HT has a pencil label “649” which could be Philpott’s prep. JSD 18/XI/83”

Material examined. Types and 67 non-type examples (61 males, 6 females. BMNH, NZAC, MONZ, CMNZ, GGNZ). See Appendix 1 for list of collection localities.

Distribution. WN / SD, NN, MB.

Flight season. 13 November to 10 February.

Remarks. Normally found in open mossy forests with good light penetration. Most sites have been in the altitude range 800–1400 m but it is known from lower levels at Ship Cove and at Karamea Bluff (420 m). Its distribution is entirely within the distribution of *acuta* but experience to date indicates it does not co-occur with that species; usually occupying a higher altitudinal station or appearing later in the season. Altitudinal separation has been noted at the same time of year in collections from the Tararua Range, Cobb Valley, Goulard Downs, Karamea and in the upper Matiri Valley. Flight period separation has been recorded from Takaka Hill, 600 m, where *acuta* occurs in November and *hamadelpha* in early January.

North Island specimens have fewer pecten bristles (8–16, total both sides: mean 25, n=10) than those from the South Island (11–22, total both sides: mean 33, n=15). This suggests that we could be dealing with incipient species here, a situation that would repay further study.

Mnesarchella hamadelpha is not easy to distinguish from *acuta* on external characters, hence the confusion of these two species by the early lepidopterists. Wing maculation is not reliable although with fresh specimens the basal ‘white’ area of *hamadelpha* is usually distinctly more ochreous than in *acuta*.

***Mnesarchella ngahuru* Gibbs, new species**

Figs 12, 72, 86, 102, 147; Map 8

Diagnosis (Figs 12, 86, 147). Male genitalia **lacking trulleum melanisation, glandular area or pecten**, and any distinctive ornamentation of the upper valve arm. Similar species: all other *acuta*-group species.

Male (Figs 12, 147). Head vestiture ochreous-white; antennae 0.64–0.66 of forewing, with 32–34 flagellomeres. Thorax dorsal vestiture pale orange-brown. Forewing 3.6–4.1 mm; dark-brown costal streak very broad with broad apex which is continuous with oblique anal fascia, basal area ochreous-white, grading to pale orange-brown toward dorsum; median costal patch ochreous-white, clearly defined; a patch of intense white scales

in centre of median area; subapical area orange-brown, often suffused with ochreous scales. Epiphysis present, small.

Female. Antennae with 26–29 flagellomeres. Forewing 3.3–3.7 mm: pale areas more suffused with white scales than in male.

Male genitalia (Figs 72, 86) (11 preparations). Trulleum with longitudinal lateral folds, but possessing neither a discrete melanised area nor a glandular pit. Valva with dorsal arm lightly melanised, truncate at apex, bearing 2–3 fine setae on upper corner and 15–20 longer, very thin setae along the medioventral side; ventral lobe also lightly melanised, about as long as arm, its posterior angle approximately a right angle; pecten absent but with 50–60 scattered setae on inner surface. Cornuti present, numerous, up to 11 pairs of small simple spines with some smaller supernumeraries, associated with 2 lightly melanised, oval sclerites. (Genitalia slide G334, Manuoha track, Waikaremoana. GGNZ.)

Female genitalia (Fig. 102) (1 preparation). Subgenital plate with a small area of microtrichia concentrated on the posterior apical prominence but leaving the margin smooth. Roof of antrum with a very extensive patch of anteriorly-directed spinules between 1/4 and 3/4 of its length, mostly comb-like but a few triangular teeth on anterior margin of patch; a trace of hexagonal patterning visible posteriorly. Ductus with comb-like spinules throughout, although very sparse at posterior end. (Genitalia microvial in glycerine, G321, Ruapehu, Morris Watt, GGNZ).

Larva indistinguishable from that of *acuta*.

Type data. Holotype: male labelled "New Zealand GB Manuoha track 1100m Urewera NP 28 Dec 1984, G.W. Gibbs"; "Holotype *Mnesarchella ngahuru* Gibbs NZAC" (red card), (NZAC).

Paratypes: 6 males, 1 female, as follows: 3 males, Manuoha track, L. Waikaremoana, GB, 950m, 28 Dec 1984. (NZAC): 1 male Gentle Annie track, Mt Holdsworth, Tararua Forest Park, 350m, WN, 17 Jan, 2000, G.W. Gibbs (NZAC); 1 female, "Ruapehu", 21, Jan, 1921, M.N. Watt, genitalia Fig. 102 (MONZ); 1 male, Mt Holdsworth, 350m, WN, 15 Jan 2011, G.W. Gibbs (MONZ); 1 male Mt Holdsworth, 350m, WN, 27 Jan 2000, G.W. Gibbs (MONZ).

Material examined. Type series plus 45 non-type examples (44 males, 2 females). See Appendix 1 for list of collection localities.

Distribution. TO, GB, WN.

Flight Season. 28 December to 6 March.

Remarks. This species occurs over a wide altitude range (350–1100 m) in forests with good light penetration. Although it may be found in the same habitat as *loxoscia* and *falcata*, its flight peak is later in the season than either of these with only an occasional overlap. (Two old females of *loxoscia* were taken at the same time as large numbers of fresh *ngahuru* males on the Manuoha track, Urewera N.P.) Its flight period coincides with that of *Mnesarchaea hudsoni* in Tongariro N.P. but the two species have not been collected from the same places.

This species was first collected by Morris Watt, a leaf-miner specialist who took a series of 27 males and 1 female on 21 January 1921 at "Ruapehu" (MONZ).

Etymology. The Māori species name ('tenth', indicating the tenth month of the Māori calendar (March) or the autumnal season) was chosen to signify the later seasonal appearance of this species, in comparison to other *acuta*-group species and to link this tiny forest moth to the indigenous language of Aotearoa.

***Mnesarchella philpotti* Gibbs, new species**

Figs 13, 73, 87, 103, 148; Map 9

Diagnosis (Figs 13, 87, 148). An *acuta*-group species **which lacks two of the typical brown markings of the *acuta*-type forewings** (subapical costal patch and the oblique brown anal fascia). Also, the upper valve arm of the male genitalia uniquely bears about **five short bulbous setae near its apex**. Similar species; all other *acuta*-group species.

Male (Figs 13, 148). Dorsal head vestiture pale ochreous-brown with darker brown-tipped scales on frons below antennal sockets, head capsule melanisation very dark, almost black; labial palps distinctly ochreous. Antennae 0.55–0.60 of forewing with 38–40 flagellomeres. Thorax dorsal vestiture pale ochreous-brown. Forewing 4.9–5.2 mm; wings slightly narrower than other *acuta*-group species, especially the hindwing, and with M1 arising from a very short stem with Rs3+4; brown costal streak begins curving away from costa at about 1/4,

leaving a narrow edging of pale ochreous-white scales; distal end of costal streak diffuse; basal area in cell ochreous-white, blending through pale ochreous to brown along dorsum, lacking a distinct brown anal fascia; median area pale ochreous-white near costa blending to ochreous-brown in centre and lacking a defined costal fascia. Fringes largely golden-brown. Hindwings pale brown with spangling of ochreous-white scales, becoming dense at apex. Epiphysis present, small.

Female. Antenna 0.51 of forewing with 30–33 flagellomeres. Forewings 4.3 mm; reduced in area in comparison to male; essentially pale ochreous-white with a strong brown crescentic costal streak and little other marking apart from some brown scales along the termen and apex.

Male genitalia (Figs 73, 87) (4 preparations). Pseudoteguminal plate lightly melanised, lacking trulleum sclerotisation but with a glandular area present. Valva with dorsal arm lightly melanised, apex slightly expanded and club-like, bearing 2–5 **short bulbous setae** around the ventral margin and 3–6 normal setae along the inner face; ventral lobe lightly melanised, about same length as arm, posterior angle broadly acute; pecten present, of 7–10 thick bristles in a short transverse central band towards median edge; a patch of 15–20 strong melanised setae between the pecten row and the apex. Vinculum elongated in ventral mid-line so that its main body (excluding lateral arms) is roughly as long as wide. **Cornuti absent**. (Genitalia slide G356, Percy Valley, GGNZ.)

Female genitalia (Fig. 103) (1 preparation). Subgenital plate with two small discrete patches of microtrichia near the posterior apex, separated by a smooth area in the mid-line. V-sclerite with an *acuta*-type anterior apex, arrowhead-like. Roof of antrum lacking patterns or spinules except for an incomplete band of plate-like spinules with comb-like edges. Ductus with spinules only towards the anterior end, posterior section free of spinules. (Genitalia G351, Percy Valley, FD, glycerine in minivial, GGNZ, specimen mislaid.)

Larva. Indistinguishable from that of *acuta*.

Type data. Holotype male labelled "New Zealand, FD, Percy Valley, 380 m, 9–10 Dec 2000 G.W. Gibbs" (white card), "Holotype *Mnesarchella philpotti* Gibbs (red card), (NZAC).

Paratypes: 4 males as follows: Percy Valley, 380m, FD, 9–10 Dec 2000, G.W. Gibbs (NZAC); 3 males, as above (MONZ).

Material examined. Type series plus 39 non-type examples (35 males, 4 females, AMNZ, MONZ, BPNZ, NZAC). See Appendix 1 for list of collection localities.

Distribution. FD.

Flight Season. 1 to 30 December.

Remarks. *Mnesarchella philpotti* occurs in southern beech forest or the subalpine shrubland zone at 380–800 m in high rainfall areas where very thick layers of periphyton smother all available surfaces. No other *Mnesarchella* species have been found co-occurring with this species.

It is possible to distinguish this species on wing characters alone because of its simplified *acuta*-type maculation. The early specimens collected by Clarke were recorded as *acuta* in his account of Lepidoptera from the Te Anau-Manapouri district (Clarke 1934) and again in Hudson (1939), hence giving the impression *acuta* extended south to Fiordland. At some stage during his work at the Cawthron Institute, Philpott made a male genitalia slide of this species (now in NZAC) but evidently too late to comment on its distinctness in his discussion of mnesarchaeid genital morphology (Philpott 1927b).

Etymology. Named to honour Alfred Philpott who pioneered the morphological study of Mnesarchaeidae.

***Mnesarchella stellae* Gibbs, new species**

Figs 14, 74, 88, 104, 149; Map 10

Diagnosis (Figs 14, 91). The largest *Mnesarchella* species, therefore the largest known mnesarchaeid. **Pecten absent but entire valva darkly melanised; dorsal arm toothed around the apex**. Similar species: all other *acuta*-group species.

Male (Figs 14, 149). Head vestiture white to ochreous-white; antennae 0.55–0.60 of forewing with 33–38 flagellomeres. Thorax dorsal vestiture pale ochreous. Forewing 4.3–5.5 mm; basal area in cell ochreous-white, blending to pale yellowish-brown along dorsum; brown anal patch small, reaching neither to costal streak nor to margin; subapical costal patch ochreous-white, elongate, nearly as long as costal streak; two patches of intense white scales in centre of subapical area; subterminal area pale brown, suffused with white. Epiphysis present, small.

Female. Antenna 0.41 of forewing with 29 flagellomeres. Forewing 4.7 mm; maculation as in male.

Male genitalia (Figs 74, 88) (8 preparations). Pseudoteguminal plate lightly melanised with thickened lateral ridges forming a slight posterior prominence on each side; trulleum not defined, glandular area absent. **Valva darkly melanised**; the dorsal arm club-like with a slightly expanded apex bearing 4–5 ‘teeth’, each with a delicate tip seta; about 15–20 longer, thin setae along medioventral edge; ventral lobe very large and spoon-like, projecting about 1/3 beyond dorsal arm; pecten absent, but inner surface densely studded with stiff bristles (>100). Cornuti present, numerous, up to 12 pairs of simple spines of small to moderate size, in 2 rows in the membrane. (Genitalia slide G523, U. Mokihinui R., GWG. NZAC).

Female genitalia (Fig. 104) (1 preparation). Subgenital plate with a small area of microtrichia concentrated on the posterior apical area. Roof of antrum with an extensive triangular patch of anteriorly-directed spinules between 1/4 and 3/4 of its length, some broad overlapping triangular teeth anteriorly but most are comb-like or single needle-like spines; a trace of the hexagonal patterning is visible posteriorly. Ductus with comb-like spinules throughout and a small cluster of spinules adjacent to the apex of the V-sclerite. (Genitalia G336, Glycerine in minivial, Karamea Bluff, GWG. GGNZ, specimen mislaid.)

Larva unknown.

Type data. Holotype male labelled "New Zealand, Surveyors Ck., Karamea Bluff, 385 m. NN, 7–8 Dec 1986 G.W. Gibbs" (white card), "Holotype *Mnesarchella stellae* Gibbs NZAC" red tag, NZAC.

Paratypes: 15 males as follows: 8 males, same collection data as holotype, G.W. Gibbs (GGNZ); 4 males NZAC; 3 males MONZ.

Material examined. Type series plus 30 non-type examples (28 males, 2 females, MONZ) See Appendix 1 for list of collection localities.

Distribution. NN.

Flight season. 7 December – 3 January.

Remarks. The three known habitats are in very wet mossy beech forest, with poor light penetration. At Karamea Bluff the site is a mere 800 m from a *hamadelpha* site but the forest is clearly different and no overlap of specimens occurred although both were common at the same time in early December. The known altitudinal range is 420–750 m.

Etymology. Named in memory of Florence Stella, G.V. Hudson's daughter who instilled a lasting entomological interest in her son (GWG).

***Mnesarchella vulcanica* Gibbs, new species**

Figs 15, 75, 89, 105, 150; Map 11

Diagnosis (Figs 15, 89, 150). An *acuta*-group species in which the **pecten bristles are grouped into a dense patch adjacent to the valve margin** at its posterior angle; valve arm distal end blunt **without finger-process**. Similar species: all other *acuta*-group species.

Male (Figs 15, 150). Head vestiture intense white to ochreous-white; antennae 0.52–0.59 of forewing with 32–33 flagellomeres. Thorax with dorsal vestiture white to ochreous-white. Forewing 4.3–4.9 mm; with basal area white to pale ochreous-white, subapical costal patch ochreous-white; a fan-like array of dark-brown fringe scales around apex containing a few white scales posterior to the apex. Epiphysis present, long.

Female. Antennae 0.40 of forewing, with 29–31 flagellomeres. Forewing 4.5 mm, not noticeably paler than male.

Male genitalia (Figs 75, 89) (15 preparations). Pseudoteguminal plate with heavily melanised trulleum mounds, spinose, separated by a **deep posterior notch, each mound with its longitudinal dimension greater than its lateral dimension**. Valva essentially unmelanised, distal end of dorsal arm bluntly rounded and bearing 2 or 3 fine setae around the apex but lacking a finger-process; ventral lobe and dorsal arm approximately equal; **pecten present, a dense oval patch of about 40–60 pointed and slightly curved bristles situated close to the posterior edge of the lobe**; posterior margin with a few strong recurved setae and proximal area of lobe with only sparse setae. Cornuti present, in two rows of 4–6 in graded sizes from small to moderate. (Genitalia slide G313, Erua-Hauhangatahi track, TO, GWG. NZAC)

Female genitalia (Fig. 105) (3 preparations). Subgenital plate smooth, lacking microtrichia. Roof of antrum lacking any melanisation but with an uninterrupted band of spinules just anterior to the hinge line, the spinules

mainly triangular teeth but including some with comb-like edges; a hexagonal pattern clearly discernable in centre, between the two lateral arms of the V-sclerite; fine, needle-like spinules in this region also. Ductus with dense comb-like spinules throughout, spinules becoming minute posteriorly in vicinity of V-sclerite apex. (Genitalia G514, glycerine in minivial, Erua track, Ruapehu. GGNZ).

Larva unknown.

Type data. Holotype male labelled "New Zealand, TO, Erua - Hauhangatahi track, 1000m, 6 Dec 1983, G.W. Gibbs" (white card), "Holotype *Mnesarchella vulcanica* Gibbs" (red card), NZAC.

Paratypes: 1 female, 8 males as follows: 1 female, unspread, Erua - Hauhangatahi track, TO, 1000 – 1100m, 31 Dec, 1978, G.W. Gibbs (NZAC); 1 male, Erua-Hauhangatahi track, TO, 1000m, 6 Dec 1983, (genital slide G313, Fig 92) G.W. Gibbs (NZAC); 1 male, Te Iringa track, Clements Road, 1000m, 19 Dec 2008, (Fig 15), G.W. Gibbs (NZAC); 1 male, Kapuni stream, TK, 1000m, 15 Dec 2002, G.W. Gibbs (NZAC); 1 male, Stratford Mountain House, TK, 800m, 16 Dec 1996, G.W. Gibbs (NZAC); 1 male, Panekiri Bluff, L. Waikaremoana, GB, 1100m, 28 Dec 1985, G.W. Gibbs (MONZ); 3 males (2 unspread), Erua-Hauhangatahi track, TO, 1100m, 6 Dec 83, G.W. Gibbs (MONZ).

Material examined. Type series plus 29 non-type examples (25 males, 4 females, NZAC, MONZ). See Appendix 1 for list of collection localities.

Distribution. TK, TO, GB, RI.

Flight season. 6 December to 19 February.

Remarks. This species was first collected by A. Philpott at 'Tongariro' in January 1930. It is a predominantly high altitude species from 800–1400 m in mossy mountane forests of all types—beech and podocarp. On the slopes of Hauhangatahi (Tongariro N.P.) and the western Kaimanawa Range it has occurred at the same time as *falcata* but at higher elevations.

The distributions of sister-species *acuta* and *vulcanica* are allopatric. This one is most likely to be confused with *falcata* since it tends to share the same habitat. Dissection is required to confirm the identity of this species.

Etymology. Named to reflect its occurrence in the vicinity of the North Island volcanoes where it was first recorded.

The *fusilella*-group of species

Three white-headed *Mnesarchella* species that differ from the *acuta*-group maculation pattern. These form a subclade—one species, unique for the genus with unicolourous bronzy forewings; the other two with a diagnostic **broad dark-brown band along the costa, extending beyond the radial vein, and running from the eye to an abrupt inwardly acute angle at 3/5**; the elongate triangular region within the cell pure white.

Male genitalic synapomorphies for *fusilella*-group include a prominent **W-shaped trulleum** around the pseudoteguminal glandular opening, its texture darkly sclerotised and pustulated. Cornuti (absent in *fusilella*) with **one or two dominant acutely pointed spines**, never multiple spines (Figs 90, 92). **Dorsal valva arms distinctly longer than ventral arms** (Figs 76–78).

Mnesarchella dugdalei Gibbs, new species

Figs 16, 76, 90, 106, 151, 152; Map 12.

Diagnosis (Figs 16, 151, 152). Forewings **uniform pale brown with a strong brassy iridescence**, devoid of markings except for **two narrow white lines**, one across the wing at 4/5, the other along termen to tornus.

Male (Figs 16, 151). All head and palp vestiture intense white, with exception of genae which are dark-brown scaled. Antennae 0.6–0.7 of forewing with 36–41 flagellomeres; scape and pedicel white with a few brown scales ventrally, flagellar scales ochreous, becoming more brownish toward tip. Thorax with long white or ochreous-white scales on pro- and meso-notum and also under head and on prosternum; tegulae ochreous above, pale brown beneath. Forewing 4.5–5.1 mm, uniform pale brown with pale brassy reflections, a narrow white transverse line at 4/5 and another narrow white line along the termen between CuA2 and M1; anal region suffused with whitish; fringes ochreous-brown, with diffuse white bands on forewing at CuP and M1 and a band of inner dark brown scales around apex interspersed with odd white scales. Hindwings pale grey-brown with faint purple reflections.

Legs with coxae ochreous-white, remainder dark-brown dorsally with a narrow ochreous band at distal end of each joint, ochreous ventrally. Tibial spurs and spines ochreous except outer spur of leg 2 which is brown. Epiphysis small. (Genitalia slide G417, male, Fairy Falls track, Waitakere Range, GWG. NZAC)

Female (Fig. 152). As for male. Antennae 0.4–0.5 of forewing with 29–30 flagellomeres.

Male genitalia (Figs 76, 90) (8 preparations). Dorsal lobes short, as wide as long. Trulleum sclerotisation present, a very broad W-shaped transverse bridge across the posterior margin of the subgenital crypt, bluntly spinose; oval glandular area conspicuous. Valva very lightly melanised; upper arm with slightly expanded distal end, rounded, with ca 24 long thin setae along its inner ventral edge; lower lobe shorter than arm, with its distal angle approximately a right angle; pecten present, a single transverse row of 18–22 strong blunt bristles across centre of lobe with 12–20 supernumerary pointed setae between pecten and apex. Cornuti present, one or two large spines on each side, sometimes with multiple points. (Genitalia G407, Fairy Falls track, Waitakere Range, AK, GWG. NZAC.)

Female genitalia (Fig. 106) (1 preparation). Subgenital plate with microtrichia over the posterior third, extending anteriorly to the transverse melanisation line of the antrum. V-sclerite with a short stem at anterior apex i.e. 'Y'-shaped. Roof of antrum with an irregular melanised band between the two arms of the V-sclerite, which bears numerous triangular teeth; situated about 1/3 from apex; antrum area with minute needle-like spinules in hexagonal pattern. Ductus with comb-like spinules towards anterior end, unadorned in posterior section. (Genitalia prep. G404, Lake Rotopounamu, GGNZ.)

Larva unknown.

Type data. Holotype male labelled "New Zealand AK Fairy Falls Track Waitakere Ra 2 Dec 1979 J.S.Dugdale" (white card), "Holotype *Mnesarchella dugdalei* Gibbs" (red card).

Paratypes: 8 males as follows: 2 males Waiomu Valley, 150m, CL, 18 Nov 2010, G.W. Gibbs (NZAC); 2 males Tapu-Coroglen Summit, 460m, CL, 18 Nov 2010, G.W. Gibbs (NZAC); 1 male Opepe Reserve, TO, 19 Dec 1991, G.W. Gibbs (NZAC); 2 males Waiomu Valley, 150m, CL, 18 Nov 2010, G.W. Gibbs (MONZ); 1 male Opepe Reserve, TO, 19 Dec 1991, G.W. Gibbs (MONZ).

Material Examined. Type series plus 48 non-type examples (38 males, 10 females; NZAC). See Appendix 1 for list of collection localities.

Distribution. AK, CL, WO, BP, TK, TO, GB, HB.

Flight season. 16 October to 21 December.

Remarks. This atypical *Mnesarchella* species has a distinctive wing colour pattern. However, its morphological and molecular characters clearly align it within the clade comprising *fusilella* and *loxoscia*. It is known from well-lit mossy forest sites between about 200 m and 1300 m and is often found in association with *fusilella* or *loxoscia*.

Etymology. Named in honour of John Dugdale who first discovered this species and to mark his outstanding contribution to the study of New Zealand's Lepidoptera.

***Mnesarchella fusilella* (Walker, 1864) new combination**

Figs 17, 23, 39, 77, 91, 107, 124–126, 128–133, 153, 154; Map 13.

fusilella Walker, 1864, p. 1008 (*Tinea*).

loxoscia sensu Hudson 1928, p. 367, pl. XXXIX, fig. 23 (*Mnesarchaea*) (misidentification).

Diagnosis (Figs 17, 153, 154). Basal anal area of forewing intense white with a broad dark-brown costal streak terminating obliquely at about 3/5 with an inwardly acute angle, **prosternum scales white**. Male genitalia: **cornuti absent**. Similar species: *loxoscia*.

Male (Figs 17, 153). Frons, vertex and postmental scales intense white; lateral area of frons between compound eye and antenna with short, closely adpressed white scales. Antennae 0.58–0.64 of forewing with 39–43 flagellomeres. Scape and pedicel white, flagellar scales usually pale ochreous above and below but occasionally brown above, becoming more brownish toward tip. Labial palps with white scales dorsally and brown ventrally, loosely scaled. Thorax dorsum and prosternum white; tegulae white-scaled except anteriorly, where brown (in alignment with costal streak). Forewings 4.5–5.1 mm, with bold white and dark-brown markings in basal 3/5; a broad brown costal streak reaching about 1/2 across chord of wing at its widest and extending to about 3/5 where it terminates obliquely forming an inwardly acute angle with the costa; an oblique brown anal fascia, situated over

the fork of CuA, extends half way across the wing from the posterior margin, its apex not quite meeting the costal streak; a slightly oblique white transverse bar crosses the median area and blends into the subapical area which is spangled with white, orange-yellow and dark-brown scales, becoming almost entirely brown toward apex. Venation with M1 arising separate from Rs3+4 stem, the cross vein r-m present at end of cell. Fringes brown with white bands on forewing at Rs1+2, M1, and CuP and an outer white patch at apex. Hindwing brownish-grey becoming darker toward apex; with slight purple reflections. Coxal joints of legs pale brown but remainder dark-brown, with a narrow ochreous band at the distal end of each joint, tarsi pale beneath, almost white. Tibial spurs brown; spines mixed brown and pale ochreous. Epiphysis normally vestigial or absent.

Female (Fig. 154). Antennae 0.44–0.50 of forewing with 36–37 flagellar segments; usually brown-scaled dorsally with ochreous scales ventrally. Forewing 4.8–5.1 mm.

Male genitalia (Figs 39, 77, 91) (17 preparations). Dorsal lobes short, about as wide as long. **Cornuti absent.** Trulleum melanisation a narrow, spinose, transverse, bilobed ('W'-shaped) bridge across the posterior margin of pseudoteguminal plate; conspicuous oval glandular pit present. Valva only very lightly melanised with apex of dorsal arm rounded, bearing ca 24 long thin setae; ventral lobe shorter than arm and with its posterior angle slightly less than a right angle; pecten present, a single transverse row of 16–22 stout blunt bristles across the centre of the lobe—left and right bristle count usually >34, but specimens from Northland may fall below this, (25–32), i.e. within range of *loxoscia*—and ca 20–30 scattered supernumerary setae between pecten and posterior angle. (Genitalia slide G402, male, Lake Okataina, GGNZ.)

Female genitalia (Fig. 107) (5 preparations). Subgenital plate with a band of microtrichia on each side around the posterior apex, leaving the mid-line free of microtrichia; microtrichiata areas extending anteriorly along lateral margins as far as the transverse melanisation line of antrum. V-sclerite with an irregular, but entire, anterior apex, sometimes with a short median stem; roof of antrum clear and membranous with some minute needle-like spinules; an incomplete melanised transverse band about half way along V-sclerite, represented by lateral patches only, with a few small comb-like spinules in roof adjacent to this band but not forming an extensive aggregation. Ductus with a dense array of comb-like spinules towards distal end but free of spinules in posterior section. (Genitalia G379, Wilton's Bush WN, GWG, in glycerine minivial, GGNZ.)

Larva (Figs 124–126, 128–133). No distinguishing features have been detected (see under *M. acuta*).

Type data. Holotype male, 'Auckland' (AK) D. Bolton. Genitalia slide no. 21780, BMNH.

Material examined. Type plus 70 non-type examples (57 males, 13 females and ?2 larvae. BMNH, NZAC, MONZ, GGNZ). See Appendix 1 for list of collection localities.

Distribution. ND, AK, WO, BP, HB, WI, WN.

Flight Season. 15 October to 26 December.

Remarks. This species was ignored for 124 years until Dugdale (1988) drew attention to the Walker specimen in BMNH. He then treated *fusilella* as a senior synonym of *loxoscia*. Since that time NPK has dissected the male *loxoscia* described by Meyrick. The present study reveals that Meyrick's *loxoscia* and Walker's *fusilella* are distinct and should be regarded as a pair of sibling species. Molecular analysis is insufficient (bootstraps, Bremer supports) to statistically confirm the relationships shown in Fig. 135. It should be noted that Hudson (1928) depicted *M. fusilella* as fig 23 of Plate XXXIX, but used the name of its look-alike sister species, *loxoscia*. None of his publications include a colour figure of *loxoscia*.

This early season species occurs in mossy forests with good light penetration and on fern-covered banks from sea-level to about 500 m. It is often found in association with *dugdalei*. Although normally diurnal, some male specimens have been taken at light. Females fly less often than males. Pairing has been observed in late morning, before noon.

Mnesarchella fusilella can be distinguished from *loxoscia* by the white scales under the head, on the tegulae and along the anal area of the forewing. However, specimens from Northland may exhibit somewhat intermediate combinations of other characters, i.e. the brown anal streak may be present and the valve pecten count is within the range for *loxoscia*. These specimens are treated here as *fusilella* because they lack cornuti and correspond with this species in all other respects. Females can be more difficult to identify due to some colour overlap in the diagnostic characters. Both members of this species pair are widely distributed in North Island, and have been found to coexist at Fairy Falls and Twin Peaks tracks, Waitakere Range AK; Mamaku Plateau BP and on the Herangi Range WO. At the latter locality and near the summit of the Waitakere Ranges (Twin Peaks), both have occurred on the same day.

At the other two places *fusilella* has been found in November, *loxoscia* in December. Further intensive collecting is needed to resolve the ecological and temporal separation of these two sister species.

***Mnesarchella loxoscia* (Meyrick, 1888) reinstated species**

Figs 18, 19, 78, 92, 108, 155, 156; Map 10.

loxoscia Meyrick 1888, p. 90 (*Mnesarchaea*); Hudson 1928, p. 367; [but note pl. xxxix, fig. 23 depicts *fusilella*]. Synonymised with *fusilella* by Dugdale 1988, p. 55.

Diagnosis (Figs 18, 155, 156): As for *fusilella* but **prosternum scales dark-brown**. Male genitalia: **two large cornuti present**. Similar species: *fusilella*.

Only the distinctions from *fusilella* are listed here since these two sister species are closely similar in many respects.

Male (Figs 18, 19, 155). Postmental scales dark-brown. Antennae with 38–41 flagellar segments, 0.6 length of forewing, flagellar scales brown above, ochreous below. Prosternum and tegulae brown scaled. Forewing length 4.5–5.2 mm (mean 4.8 mm), with the central white area in the cell distinctly ochreous, not intense white, and with a strong brown streak along the anal margin from base to nearly reach the oblique brown anal fascia.

Female (Fig. 156). Postmental scales dark-brown. Antennae with 31–35 flagellar segments, scale colour as in male. Prosternum dark-brown but tegulae variable—white, brown or mixed. Forewing 4.4–4.7 mm; brown anal streak variable, may be suffused with white scales, or absent.

Male genitalia: (Figs 78, 92) (15 preparations). Glandular area present. Pecten consists of a single transverse row of 12–18 bristles across middle of valva, total pecten bristle count <34. **Cornuti present**, two only, large, conspicuous and often multipointed. (Genitalia slide G368, Table Mountain, Kaueranga valley, Thames, GWG. NZAC.)

Female genitalia (Fig. 108) (2 preparations). Subgenital plate with an extensive field of microtrichia over the apical half, continuous across the centre-line and with the transverse melanisation line of the antrum; lateral margin of subgenital plate with a small blunt spine slightly posterior to the melanisation line. Apex of V-sclerite fragmented. Antrum roof sparsely adorned with single needle-like spinules over the widest part of the V-sclerite, grading into larger comb-like spinules across the anterior section of the V. Ductus with spinules throughout but sparse and very small in posterior part. (Genitalia G359, Mnauoha track, L. Waikaremoana, GWG, glycerine in minivial, GGNZ.)

Larva. Has not been differentiated from other *acuta*-group larvae.

Type data. Lectotype male (designated by Dugdale 1988: 55), Auckland (AK), 22 Dec. 1885, E. Meyrick (specimen 15/15 in Meyrick collection). Male genitalia slide no. 23422 BMNH. Note: this specimen is incorrectly listed as female in Dugdale (1988).

Material examined. Type plus 38 non-type examples (34 males, 4 females. BMNH, NZAC, MONZ, GGNZ). See Appendix 1 for list of collection localities.

Distribution. ND, AK, CL, WO, BP, TK, TO, GB, RI, WN / SD.

Flight season. North Island: 4 December to 15 January; South Island specimens are outliers in October.

Remarks. See Remarks for *M. fusilella* above regarding the history of nomenclature for *fusilella* and *loxoscia*.

Mnesarchella loxoscia occurs in similar habitats to *fusilella* but reaches altitudes of up to 1100 m. It has been found in association with *vulcanica* and *dugdalei* in the Tongariro N.P.; with *acuta* near Wellington and with *fusilella* in the Waitakere and Herangi Ranges and on the Mamaku Plateau. Normally it seems to fly later in the season than *fusilella* but both species have been taken on the same day: 1 December near the summit of the Waitakere Ranges (Twin Peaks) AK by R.J.B. Hoare, and 10 December on the Herangi Range WO by J.S. Dugdale. There is a single record of two males from Pelorus Bridge in the South Island, sweepnetted by J.S. Dugdale in October 1970 (NZAC). Males have occasionally been taken at light.

Females of *loxoscia* seem to be more variable than males with respect to their colour distinctions from *fusilella*. However, in those examined, the scales under the head are invariably dark-brown, which proves to be the best diagnostic feature since these scales are present in even the most worn specimens.

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Appendix 1. Localities of specimens examined

The following list usually omits the collector's name and date, except for primary type specimens, whose full data is given in bold. Also, specimens in the G.V. Hudson collection (kept separately in MONZ) are annotated 'GVH' and historic specimens from the Philpott collection in NZAC are annotated 'AP'. Old specimens with vague locality information are noted as being from, e.g., "Auckland", or in some cases omitted altogether where unambiguous localities can be substituted. The repositories of specimens are listed in parentheses according to the abbreviations on p. 16.

***Mnesarchaea fallax* Philpott, 1927**

North Island. TO. Mahuia campsite, 880 m, Tongariro National Park (GGNZ); Erua-Hauhangatahi track, 800 m, Tongariro National Park (GGNZ). **TK.** U. Kapuni Valley, 1000 m, Mt Taranaki National Park (GGNZ). **South Island. NN. Mount Arthur Tableland, 10 Dec 1928, A Philpott (NZAC);** U. Maitai Road, Nelson, 260 m (GGNZ); Goulard Downs, 620 m, Kahurangi National Park (GGNZ); Canaan, 740 m, Takaka Hill (GGNZ); Cobb Ridge track, 800 m (NZAC); Lake Aorere, 1030 m, Kahurangi National Park (NZAC); Karamea Bluff, 317 m, Kahurangi National Park (GGNZ). **BR.** Lewis Pass, 875 m (GGNZ); Cave Creek track, 90 m, Bullock Creek (GGNZ).

***Mnesarchaea fusca* Philpott, 1923**

South Island. NN. Goulard Downs, 7 Feb 1922, A. Philpott (NZAC); Fenian track, Karamea, 150 m, Kahurangi National Park (NZAC); Dun Mountain, 1000 m (NZAC, AP); U Maitai Valley, 200 m, Nelson (NZAC, AP); Lake Rotoroa, 500 m, Nelson Lakes National Park (NZAC, AP); Pigeon Saddle, 500 m, Abel Tasman National Park (NZAC); Tonga Quarry, 20 m, Abel Tasman National Park (GGNZ). **SD.** Picton Reservoir, 60 m, Waitohi Valley (GGNZ).

***Mnesarchaea hudsoni* new species**

North Island. AK. Quarry track, Waitakere Range, 250 m (NZAC). **CL.** Summit track, 530 m, Little Barrier Island (GGNZ); Tapu-Coroglen Saddle track, 440 m, Coromandel Ra (GGNZ). **BP.** Kaimai Saddle, 500 m, (NZAC); Manganuku Gorge track, 200 m, Te Urewera National Park (GGNZ). **TO.** Poronui, 790 m, Kaimanawa Forest Park (NZAC); Lake Rotopounamu, 740 m, Tongariro National Park (GGNZ). **GB.** Lake Waikareiti track, 700 m (GGNZ). **HB.** Triplex Hut, 550 m, Eastern Ruahine Forest Park (GGNZ). **WN. Otari-Wilton's Bush Reserve, 80 m, Wellington 7–9 Mar 1922, G.V. Hudson (MONZ);** Penn Creek, 600 m, Tararua Forest Park (IHNZ); Otaki Forks, 140 m, Tararua Forest Park (GGNZ); Roaring Meg Creek, 100 m, Tararua Forest Park (IHNZ, GGNZ); Donnelly's Flat, 400 m, Tararua Forest Park (GGNZ); Whakanui track, 150 m, Rimutaka Forest Park (GGNZ); Rimutaka Hill Summit, 500 m, Rimutaka Forest Park (IHNZ, GGNZ); Muritai Park track, 160 m, East Harbour Regional Park (GGNZ); Gollans Valley, 120 m, East Harbour Regional Park (GGNZ). **WA.** Tauanui Valley, 200 m, Aorangi Range (IHNZ).

***Mnesarchaea paracosma* Meyrick, 1886**

South Island. KA. Fyffe-Palmer Reserve, 150 m (NZAC); Puhipuhi Scenic Reserve, 180 m, (GGNZ); Black Millar Stream, 20 m, Okiwi Bay, Kaikoura (CMNZ); Goose Bay, 20 m, Kaikoura (CMNZ). **MC.** Kaituna, Banks Peninsula (CMNZ); Governors Bay, Lyttleton (CMNZ); Prices Bush, 40 m, Banks Peninsula (CMNZ); Mt Pleasant, 420 m, Port Hills (GGNZ); Craigieburn, 765 m (BPNZ). **MK.** Hooker Road bridge, 700 m, Mt Cook National Park (GGNZ); Mt Cook Village, 800 m (BPNZ). **SC.** Kelceys Bush, 220 m, Waimate (BPNZ). **DN.** Sandymount, 320 m, Dunedin (CMNZ); Bradford, 100 m, Dunedin (GGNZ); Botanical Gardens, 40 m, Dunedin (BPNZ); Mt Cargill, 676 m, Dunedin (BPNZ); Swampy Spur, 650 m (BPNZ); Leith Valley, 300 m, Dunedin

(BPNZ); Evansdale Glen, 20 m, Blueskin Bay (BPNZ); Waitati, Blueskin Bay (BPNZ); Silver Peaks, 750 m (BPNZ); Maungatua Hills, 700 m, West Taieri (BPNZ); Tunnel Beach, Dunedin (BPNZ); Watson's Beach, 20 m (BPNZ); Waipori Falls, Lammerlaw Range (BPNZ). **CO.** Dansey's Pass, 520 m (BPNZ); Roaring Meg Station, 220 m (BPNZ); Craig Flat, 60 m, Clutha Valley (BPNZ); above Waikaia Bush, 1200 m, Old Man Range (BPNZ); Luggate Ck, 785 m (BPNZ). **OL.** "Lake Wakatipu", 320 m, 15 Dec 1882, E Meyrick (BMNH); 12-mile Ck, 315 m, Lake Wakatipu (BPNZ); Kinloch-Greenstone roadside, 320 m, L. Wakatipu (BPNZ); Glacier Burn, 900 m (GGNZ); Mt Alfred track, 500 m (GGNZ); Earnslaw Burn, 380 m, Diamond Lake (GGNZ); Turret track, 560 m, Chinaman's Flat (GGNZ); Bob's Peak track, Queenstown (BPNZ); The Gorge, 400 m, Queenstown (PMcQ); Lake Luna, 820 m (NZAC); Otago Boys High Lodge, 480 m, Matukituki Valley (GGNZ). **SL.** False Islet, 85 m, Catlins (BPNZ); Princhester Ck, 500 m, Takitimu Ra. (GGNZ); Tarangatua Reserve, 200 m (GGNZ); Dolamore Peak, 180 m, Hokonui Hills (NZAC); Oreti Beach, 5 m (BPNZ). **FD.** Borland Valley, 280 m (GGNZ); Eglinton Valley, Fiordland National Park (BPNZ); Lake Manapouri, 200 m (CMNZ).

***Mnesarchella acuta* (Philpott, 1929)**

North Island. **RI.** Pohangina Gorge, 420 m, Ruahine Forest Park (IHNZ). **WN.** Ohau Gorge, 200–320 m, Tararua Forest Park (GGNZ); Yeate's track, 350–750 m, Ohau Valley, Tararua Forest Park (GGNZ); Saddle Ck, 300–400 m, Waitatapia Valley, Tararua Forest Park (GGNZ); Field hut track, 700 m, Tararua Forest Park (IHNZ); Kapakapanui track, 150 m, Tararua Forest Park (GGNZ); Holdsworth Lodge, 320 m, Tararua Forest Park (GGNZ); Wainuiomata Reservoir, 140 m (MONZ, GVH); 5-mile track, 180 m, Rimutaka Forest Park (GGNZ); Hawtrey Summit, 320 m, East Harbour Regional Park (GGNZ). **South Island.** **SD.** Pelorus Bridge, 30 m (NZAC, AP); Grove Road, 60 m, Queen Charlotte Sound (MONZ, GVH); Picton Reservoir, 60m, Waitohi Valley (GGNZ); Tennyson Inlet, 10 m, Pelorus Sound (NZAC); Maud Island, 40 m, Pelorus Sound (GGNZ). **NN.** Reservoir Camp, 100 m, Nelson (GGNZ); Dun Mountain track, 550 m, Nelson (GGNZ); Dun Mountain, Nelson (NZAC, AP); U Maitai – Maungatapu Saddle, 300 m, Nelson (GGNZ); Red Hills Hut, 900 m, Richmond Range (GGNZ); Knuckle Hill, 145 m, Whanganui Inlet (GGNZ); Oparara Valley track, 200 m, Karamea (GGNZ); Totaranui Hill roadside, 250 m, Abel Tasman National Park (GGNZ); coastal track, 10 m, Abel Tasman National Park (GGNZ); Takaka Hill road, west side, 600 m (GGNZ); Canaan, 800 m, Takaka Hill (GGNZ); Riwaka Valley, 100 m (IHNZ, NZAC); Brown Hut, 140 m, Heaphy track (GGNZ); Lewis Valley, 50–150 m, Heaphy track (GGNZ); Scotts Beach track, 100 m, Karamea (GGNZ); Crow Hut, 310 m, Karamea Valley (NZAC); Denniston Plateau, 150–500 m (NZAC); Station Ck, 510 m, Big Bush (GGNZ); Lake Matiri, 400 m, Matiri Valley (GGNZ). **MB.** Pine Valley track, 300–400 m, Richardson Range (GGNZ). **BR.** Ada Pass, 960 m, U Maruia R (GGNZ); Lewis Pass, 870 m (GGNZ); Stoney Ck, W Inangahua State Forest (NZAC); Fletcher's Ck, W Inangahua State Forest (NZAC); Mawhera State Forest, 300 m (NZAC); Rahu Saddle, 680 m, Reefton (GGNZ); Lake Rotoiti lakeside track, 650 m, Nelson Lakes National Park (GGNZ); Cape Foulwind, 40 m (NZAC); Tiropahi R. 160 m., Paparoa National Park (GGNZ); Lake Brunner, 100m (NZAC, GGNZ); Pororari Valley, 60 m, Punakaiki (GGNZ); Fox River, track to cave, 100 m (GGNZ). **KA.** Puhipuhi Scenic Reserve, 140 m (GGNZ); Claverly, 10 m, N of Conway River mouth (CMNZ). **NC.** "Arthurs Pass", 750 m, 9 Jan 1920, A. Philpott (NZAC); U Bealey Valley, 900 m (GGNZ); Klondyke Corner, 650 m, Waimakariri Valley (GGNZ); Mt Grey (CMNZ); White Rock (CMNZ). **WD.** Otira, 450 m (MONZ, GVH); Frosty Ck, Lake Mahinapua, 20 m (GGNZ); Mt Greenland, 750 m (NZAC); Franz Josef Glacier, 150 m (NZAC); Robert Point track, Franz Josef, 200 m (GGNZ); Franz-Fox roadside, 350 m (GGNZ); Lake Matheson, 150 m, Fox Glacier (GGNZ); Welcome Flats Hut, 420 m, Copeland R. (GGNZ).

***Mnesarchella falcata* new species**

North Island. **WO.** Mangaohae Stream, 200 m, Waitanguru (GGNZ); Whakapatiki Stream, 160 m, Herangi Range (NZAC). **TO.** Kakahu Camp, 500m, Pureora Forest Park (GGNZ); Te Iringa hut track, 800m (GGNZ); Lake Rotopounamu, 720m, Tongariro National Park (GGNZ); Te Ponanga Saddle, 750m, Tongariro National Park (GGNZ); Waitonga Falls track, 1200 m, Tongariro National Park (NZAC); Silica Falls track, 1350 m, Tongariro National Park (NZAC); Mangawhero River tributary, 900 m, Tongariro National Park (GGNZ); **Ranger Station, Ohakune, 650m, Mangawhero R. Tongariro National Park, 7 Dec 1983, G.W. Gibbs (NZAC, GGNZ);** Erua

track, Hauhangatahi, 800m, Tongariro National Park (GGNZ). **RI.** Lake Colenso, 740m, Ruahine Forest Park (IHNZ); Purity Hut, 1100m, Ruahine Forest Park (GGNZ). **HB.** Track to Bell Rock, 900 m, Boundary Stream Reserve (NZAC).

***Mnesarchella hamadelpha* (Meyrick, 1888)**

North Island. WN. Dundas Hut basin, 800 m, U Ruamahanga River, Tararua Forest Park (GGNZ); track to Pukematawai Peak, 800–1200 m, Western Tararua Range (GGNZ). **South Island. NN. Mt Arthur, 2,800–3,500 ft, 9 Jan 1886, E Meyrick (BMNH);** Flora Hut, 850 m, Arthur Range (NZAC, CMNZ); Flora River (NZAC); Cobb Valley Powerhouse, 200 m, Takaka (GGNZ); road to Cobb Dam, 900 m (GGNZ); Asbestos track, Cobb Dam road (NZAC, GGNZ); Heaphy track, 300 m, Aorere Valley (GGNZ); Goulard Downs, 800 m (GGNZ); Mt Arthur Tableland, 1400 m (NZAC); Herbert Range, 1020 m, Kahurangi National Park (GGNZ); Takaka Hill road, W side, 600 m (GGNZ); Canaan, 730 m, Takaka Hill (GGNZ); View Hill Saddle, 420 m, Karamea Bluff (GGNZ); U Matiri Valley, Murchison, 1100 m (GGNZ); Lake Rotoroa, Nelson Lakes National Park (NZAC, MONZ); U Maitai Valley, Nelson (NZAC); Dun Mountain, 950 m, Nelson (NZAC, MONZ); New Creek, 100 m, Buller Gorge (NZAC). **SD.** Ship Cove, 20 m, Queen Charlotte Sound (NZAC). **MB.** Pine Valley track, 300–500 m, Richmond Range (GGNZ).

***Mnesarchella ngahuru* new species**

North Island. GB. Manuoha track, 950 m, Lake Waikaremoana, Te Urewera National Park, 28 Dec 1984, GW Gibbs (GGNZ, NZAC); Rahui Island, Lake Waikareiti, 878 m (GGNZ); Panekiri Bluff track, 870 m, Lake Waikaremoana (GGNZ). **TO.** Lake Rotopounamu, 850 m, Tongariro National Park (IHNZ); Te Ponanga Saddle, 750 m, Tongariro National Park (GGNZ); ‘Ruapehu’ MN Watt (MONZ); Erua-Hauhangatahi track, 750 m, Tongariro National Park (GGNZ); Blythe Hut track, Ruapehu, 1200 m (E.S. Nielsen, GGNZ); Forest Walk, Ohakune Visitor Centre (NZAC); Lake Rotokura, 712 m, Ohakune (NZAC); Silica Falls track, 1350 m, Tongariro National Park (NZAC). **WN.** Gentle Annie track, 350 m, Mt Holdsworth, Tararua Forest Park (ES Nielsen, GGNZ).

***Mnesarchella philpotti* new species**

South Island. FD. Milford track (Fenwick) (MONZ); McKinnon pass, Milford track (CE Clarke) (MONZ); Chester Burn, 750–800 m, Murchison Mountains (BPNZ); **Percy Valley, 800 m, Lake Manapouri, 10 Dec 1988, GW Gibbs (GGNZ, NZAC);** Percy Valley saddle road, 380 m (GGNZ); Grono Spur, 860 m, Secretary Island, Doubtful Sound (larvae) (GGNZ).

***Mnesarchella stellae* new species**

South Island. NN. Surveyors Creek, Karamea Bluff road, 380 m, Kahurangi National Park, 7–8 Dec 1986, GW Gibbs (GGNZ, NZAC). Fenian track, 100m, Oparara Basin, Karamea (GGNZ); Surveyors Creek, 384 m, Karamea Bluff road (GGNZ); tributary of U Mokihinui River, 750 m, Kahurangi National Park (GGNZ).

***Mnesarchella vulcanica* new species**

North Island. TO. Erua-Hauhangatahi track, 1000 m, Tongariro National Park, 6 Dec 1983, GW Gibbs; Waipakihi Valley, 950 m, Kaimanawa Forest Park (GGNZ); Waihohonu Bush, 1150 m (GGNZ); ‘Tongariro’ (CE Clarke) (AMNZ); Mahuia Camp, 880 m, Tongariro National Park (IG Andrew); Mangawhero Stream, 920 m (GGNZ); Te Iringa hut track, 950 m, Kaimanawa Forest Park (GGNZ). **GB.** Panekiri Bluff, 1200 m, Lake Waikaremoana (GGNZ). **TK.** Pouakai-Ahukawakawa Swamp border, 930 m (NZAC); Pouakai Range, 1250–1400 m, Mt Taranaki National Park (NZAC); Kapuni Valley, 1100 m, Mt Taranaki (NZAC); Stratford Mountain House,

850 m (GGNZ). **RI.** Sunrise Hut Track, 880 m, eastern Ruahine Forest Park (GGNZ); Rangiwahia track, 1000 m, Ruahine Range (IG Andrew).

***Mnesarchella dugdalei* new species**

North Island. AK. Fairy Falls track, 250 m, Waitakere Range, 2 Dec 1979, J.S. Dugdale. (NZAC); also Cascades track, Kauri Knoll, Upper Huia Dam track, Waitakere Ra. 200–300 m (NZAC); Cosseys Gorge, Hunua Range (NZAC), Kohukohunui track, Hunua Range (NZAC). **CL.** Moehau, 400m, Coromandel Range (GGNZ); Tapu road Summit track, 500m, Coromandel Ra. (NZAC, GGNZ); Kauri Dam, 300m, also Tarawaere Stream, 190 m, Kauaeranga Valley (GGNZ); track to Kaitarakahi Summit, 5–600 m, Coromandel Range (NZAC). **WO.** Mangatarata Stream, 300 m, Hapuakohe Range (NZAC); Mangatoa Saddle, 120m, Herangi Range (NZAC); Whakapatiki Stream, 160 m, U Awakino Valley (NZAC). **BP.** Mamaku Plateau, 550 m (GGNZ). **TO.** Opepe Reserve, 720m (NZAC, GGNZ); Te Ponanga Saddle, 750 m (GGNZ); Lake Rotopounamu, 750m, Tongariro National Park (GGNZ); Ketetahi track, 1000 m, Tongariro National Park (GGNZ); Mahuia campsite, 880 m, Tongariro National Park (GGNZ); Waipakihi road end, 960m, Kaimanawa Forest Park (GGNZ); Mahuia Campsite, 880 m, Tongariro National Park (NZAC, GGNZ); Whakapapanui track, 1000 m, Tongariro National Park (NZAC). **GB.** Old Maori track to Kaitawa, 600 m, Lake Waikaremoana (NZAC). **HB.** Boundary Stream Reserve, 400–500 m, Hawkes Bay (NZAC). **TK.** Mt Taranaki South side, 610m (NZAC); Waitaanga plateau, 400m, Mt Taranaki National Park (MV light) (NZAC).

***Mnesarchella fusilella* (Walker, 1864)**

North Island. ND. Wairau Summit, 390–460 m, Waipoua Forest (NZAC); Waipoua Forest (MV light) (NZAC). **AK.** “Auckland”, **D. Bolton (BMNH)**; Fairy Falls track, 250 m, Waitakere Range (NZAC), also Kauri Knoll, Kauri Grove track, Quarry-Forbes-Centennial track loop, Cascade track, Cutty Grass track, Spragg’s Bush, Twin Peaks track, Tom Thumb bypass track (NZAC); Hunua Gorge, 100m, Hunua Range (BPNZ); also Wairoa-Cosseys track, Kohukohunui track, Suspension bridge track, Hunua Range (NZAC). **CL.** Waiomu Valley track, 200 m (NZAC); Tapu-Coroglen Summit, 500 m (GGNZ); Tarawaere Stream, 190 m, Kauaeranga Valley (GGNZ). **WO.** Mangatoa Saddle, 120m, Herangi Range (NZAC). **BP.** Mt Te Aroha, 616–924 m, Kaimai Range (NZAC); Mamaku Plateau roadside, 550 m (GGNZ); Lake Okataina roadside, 400 m (GGNZ); Wairere Falls, 320 m, Tarawera (GGNZ). **HB.** White Pine Bush, 250 m (NZAC); **TK.** Puketi Trust Lodge (MONZ). **TO.** Raurimu (MONZ). **WI.** Bruce Park Scenic Reserve, 250 m (GGNZ). **WN.** Otaki Forks, 140 m, Tararua Forest Park (GGNZ); Otari-Wilton’s Bush, 80 m, Wellington City (MONZ, GVH, GGNZ); Muritai Park track, 100 m, East Harbour Regional Park (MONZ, GVH); Sunny Grove, Wainuiomata; Whakanui track, 150 m, Rimutaka Forest Park (GGNZ).

***Mnesarchella loxoscia* (Meyrick, 1888)**

North Island. ND. Hauturu trig track, 700 m, Waima Forest (GGNZ). **AK.** ‘Auckland’ 22 Dec 1885, E Meyrick (BMNH); Cutty Grass track, 380 m, Waitakere Range (NZAC); also Twin Peaks track; Scenic Drive; Fairy Falls track; Walkers Bush at UV light (all Waitakere Range) (NZAC). **CL.** South branch, Kaiarara Stream, 200–400 m, Hiraikimata (Mt Hobson), Great Barrier Island (GGNZ); Moehau, 300–890 m, Coromandel (GGNZ); Tapu Saddle, Crosby’s track, 500 m, Coromandel Range (GGNZ); Waiomu Valley, 200 m (NZAC, GGNZ); track to Kaitarakahi Summit, 500–600 m, Kauaeranga Valley (NZAC); Table Mountain, 600–800 m, Kauaeranga Valley (GGNZ). **WO.** Mangatoa Saddle, 120 m, Herangi Range, south of Marakopa (NZAC); Mangapohue Valley, 200 m, 21 km W Waitomo (NZAC); Te Miro Reserve, 220 m, 12 km NE Cambridge (GGNZ); Waitanguru, 200 m, Herangi Range (GGNZ); U Awakino Valley, 100–250 m, Mahoenui (N Hudson) (GGNZ). **BP.** Mt Ngongotaha, 750 m, Rotorua (NZAC); Tarukenga Scenic Reserve, 500 m, Mamaku Plateau (NZAC); Galaxy Road, 560 m, Mamaku Plateau (NZAC). **TO.** Mt Pureora, 670–1170 m (NZAC); ‘Ohakune’ (GV Hudson) (BMNH); Erua-Hauhangatahi track, 800 m, Tongariro National Park (GGNZ); Clements Road, 800 m, Kaimanawa Forest Park (GGNZ) **GB.** Panekiri Bluff summit, 1170 m, Lake Waikaremoana (GGNZ); Waipaoa Hut, 600 m, Lake Waikaremoana (GGNZ); Manuoha track, 650–800 m, Lake Waikaremoana (GGNZ). **TK.** Pukeiti Trust Reserve, 350 m, Mt Taranaki (TH

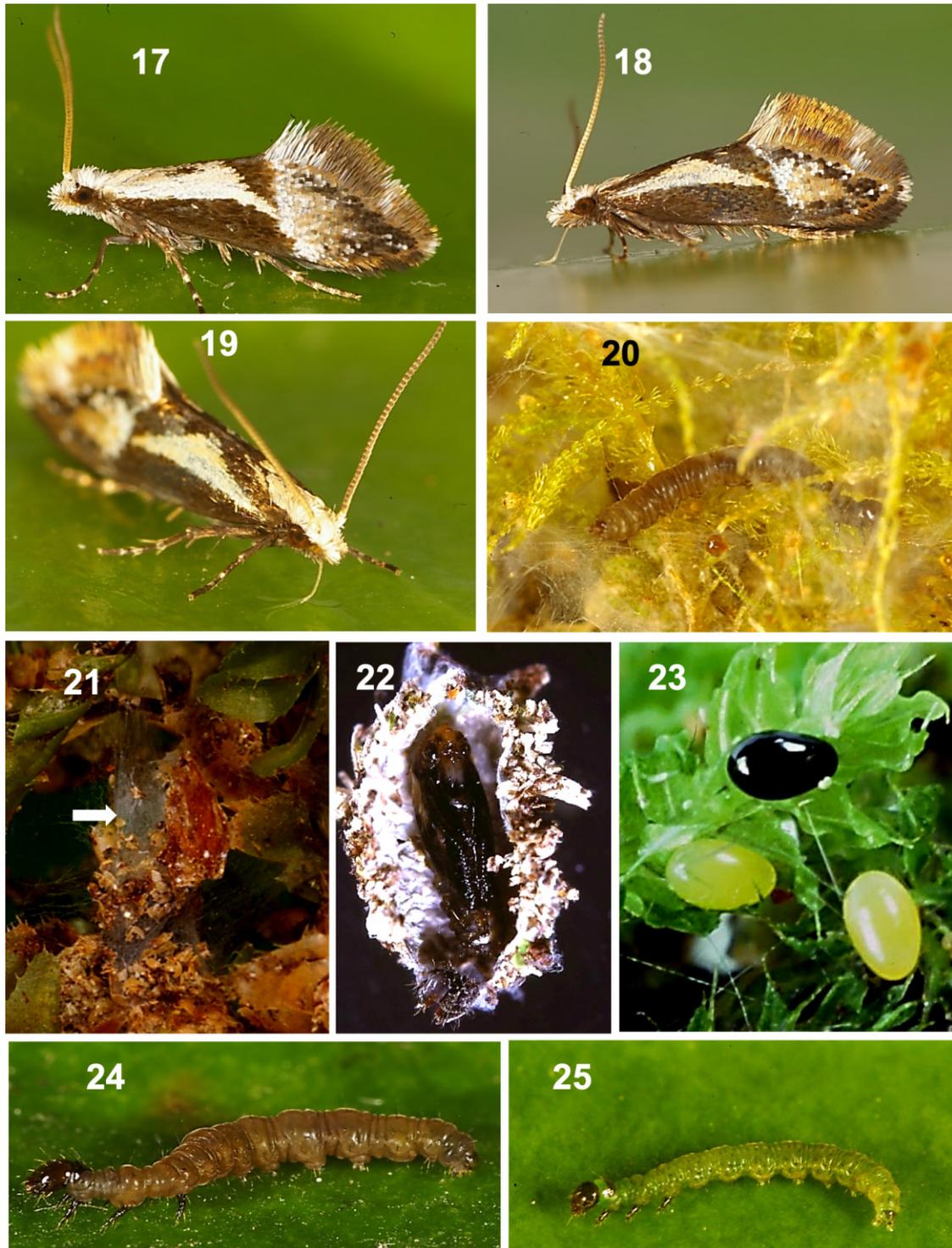
Davies); Waitaanga Plateau, 520 m, 2 km W Waitaanga; Ahitihi, 80 m, Taranaki (NZAC); Waitewhenua Stream, 210 m, 21 km N Ohura (NZAC). **RI.** Knight's track, 750 m, SW Ruahine Range (GGNZ); Mangoira Stream road bridge, East Mangahuia Road, 550 m, SW Ruahine Range (GGNZ). **WN.** 'Kaitoke' (GV Hudson) (MONZ); 5-mile track, 100–180 m, Rimutaka Forest Park (GGNZ). **South Island. SD.** Pelorus Bridge, 40 m (NZAC).



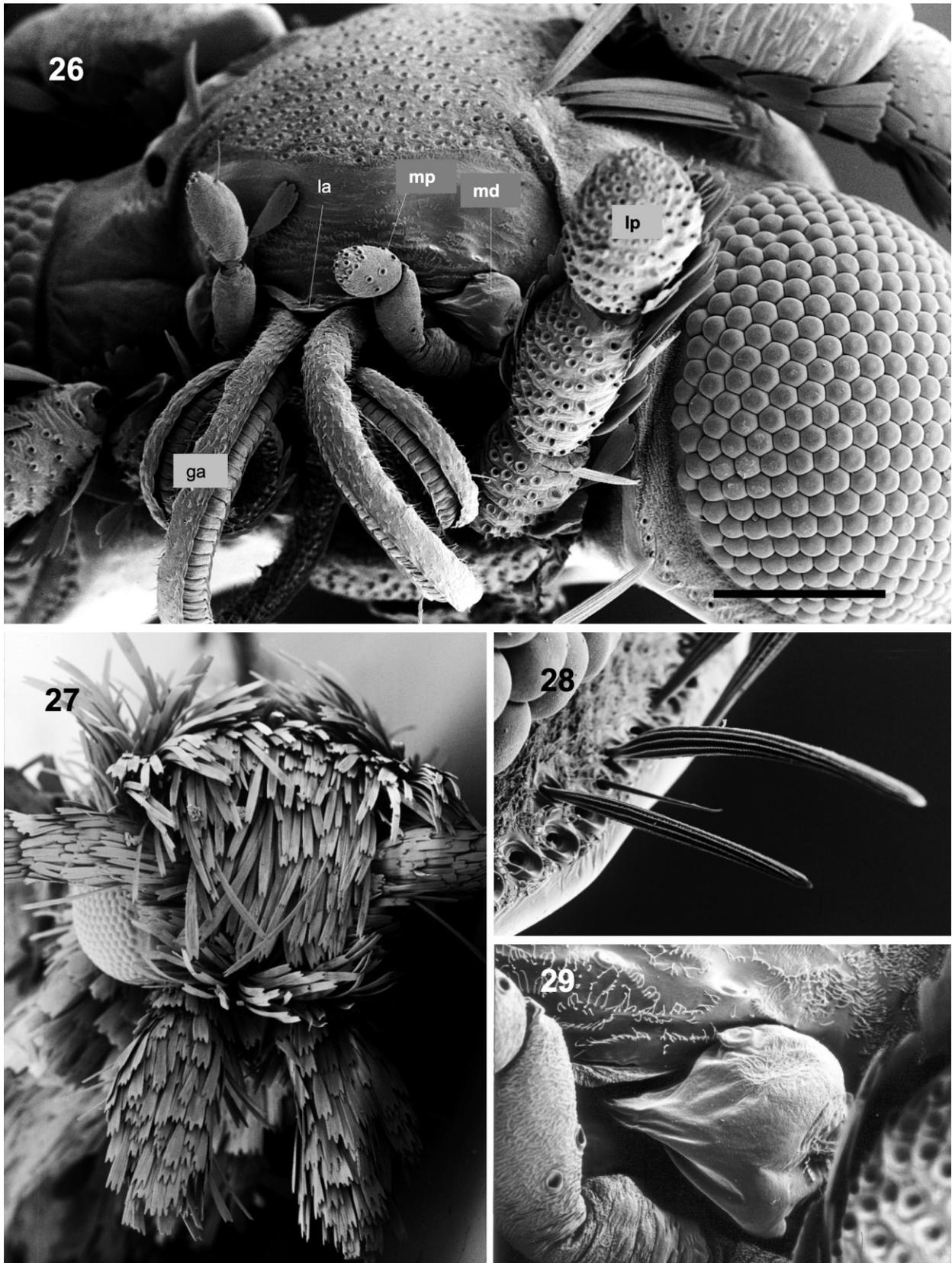
Figs 1–19. Living adults of Mnesarchaeidae. (1–8) adults of *Mnesarchaea*: 1 male *M. fallax*, Lewis Pass BR (fwl 4.5 mm); 2 female *M. fallax*, Lewis Pass BR (fwl 4.0 mm); 3 male *M. fusca*, Waitohi Valley, Picton Reservoir track, SD (fwl 3.3 mm); 4 female *M. fusca*, Waitohi Valley, Picton, SD (fw 3.2 mm); 5 male *M. hudsoni*, Otaki Forks, Tararua Ra, WN (fwl 4.0 mm); 6 female *M. hudsoni*, Sunrise track, Ruahine Ra, RI (fwl 4.0 mm); 7 male *M. paracosma*, Glacier Burn, L. Wakatipu, OL (fwl 3.8 mm); 8 female *M. paracosma*, Glacier Burn, OL (fwl 3.5 mm).



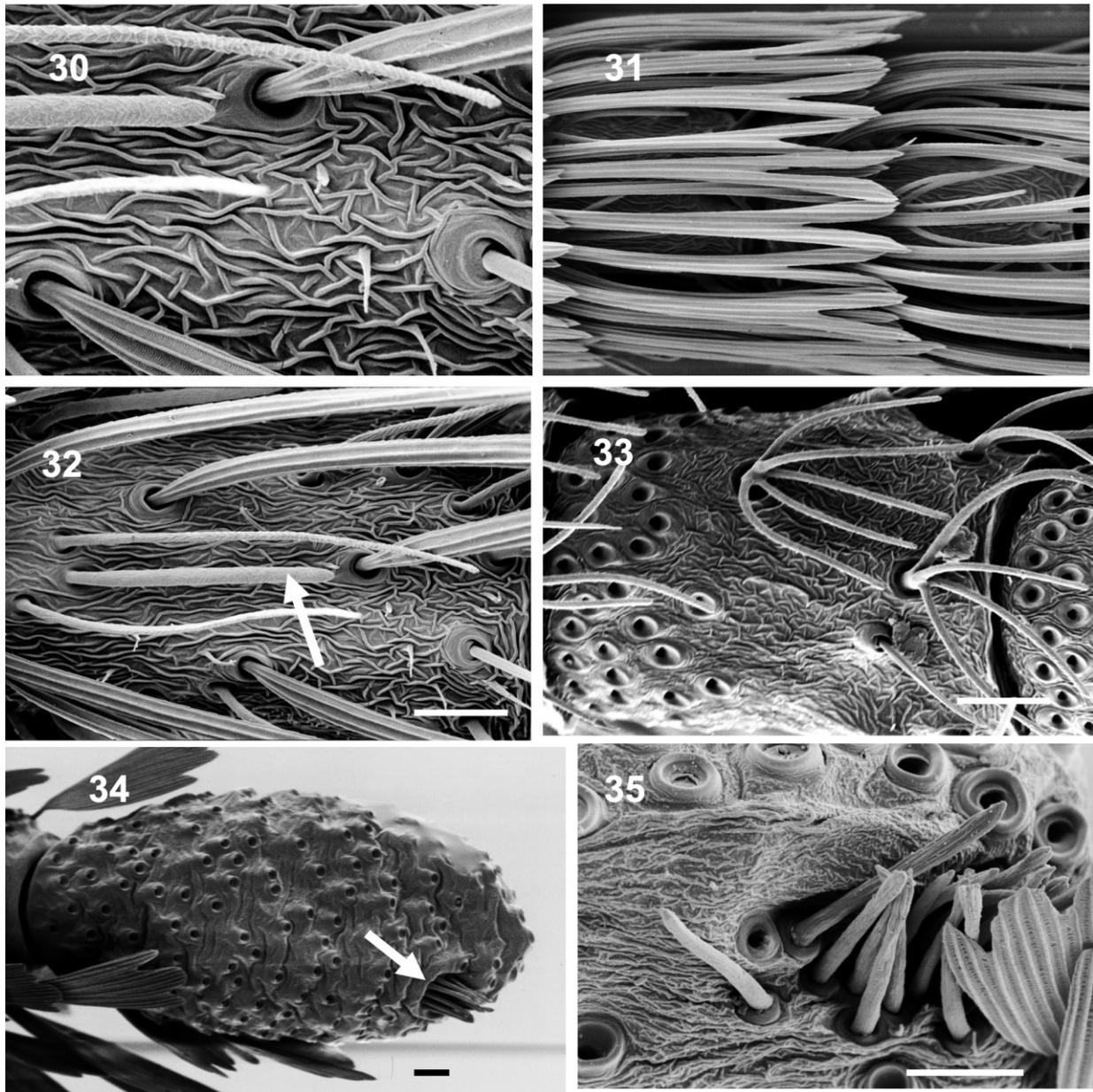
(9–16) Live adults of *Mnesarchella*: 9 female *M. acuta*, Pororari Valley, BR (fwl 4.7 mm); 10 male *M. falcata*, Kaukore Reserve, TO (fwl 4.6 mm); 11 male *M. hamadelpa*, Pine Valley, MB (fwl 4.8 mm); 12 male *M. ngahuru*, Mt Holdsworth, Tararua Ra, WN (fwl 3.8 mm); 13 male *M. philpotti*, Percy Valley, FD (fwl 5.1 mm); 14 male *M. stellae*, Surveyor's Ck, Karamea Bluff, NN (fwl 5.0 mm); 15 male *M. vulcanica*, Te Iringa track, TO (fwl 4.6 mm), 16 male *M. dugdalei*, Waiomu Valley, CL (fwl 4.8 mm).



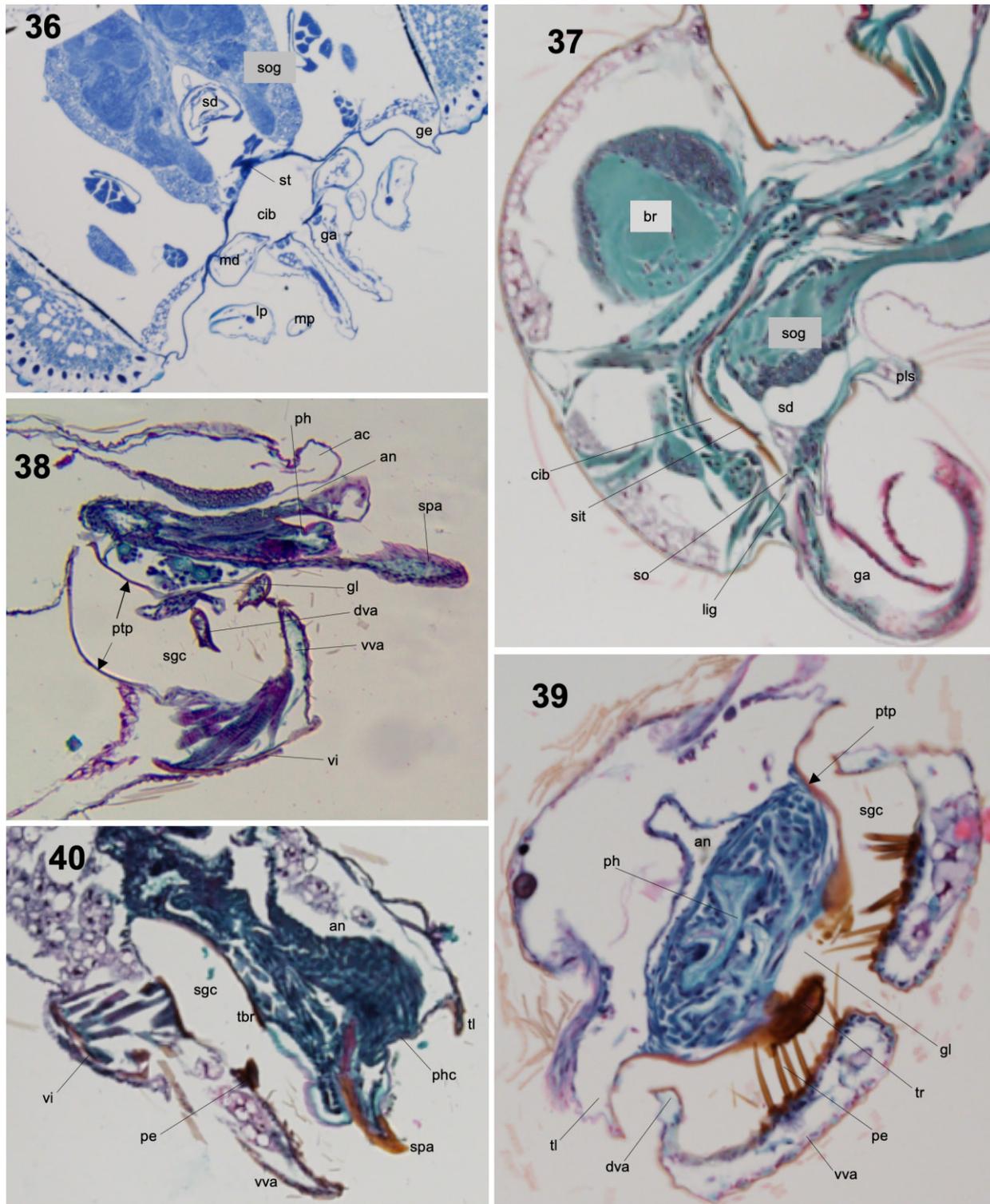
(17–19) Live adults of *Mnesarchella*: 17 male *M. fusilella*, Wainuiomata Valley, WN (fwl 4.8 mm); 18 male *M. loxoscia*, Waiomu Valley, CL (fwl 5.0 mm); 19 male *M. loxoscia* with tongue extended into droplet of water. **Figs 20–25** *Mnesarchaeidae* immature stages: 20 mature larva of *Mnesarchella acuta* within its silken tunnel system; 21 *M. acuta* cocoon under construction; 22 cocoon of *M. acuta* opened to show pupa in situ; 23 eggs of *M. fusilella* on second day, black one fertile with sclerotized chorion; 24 mature larva of *M. acuta*; 25 submature larva of *Mnesarchaea paracosma*.



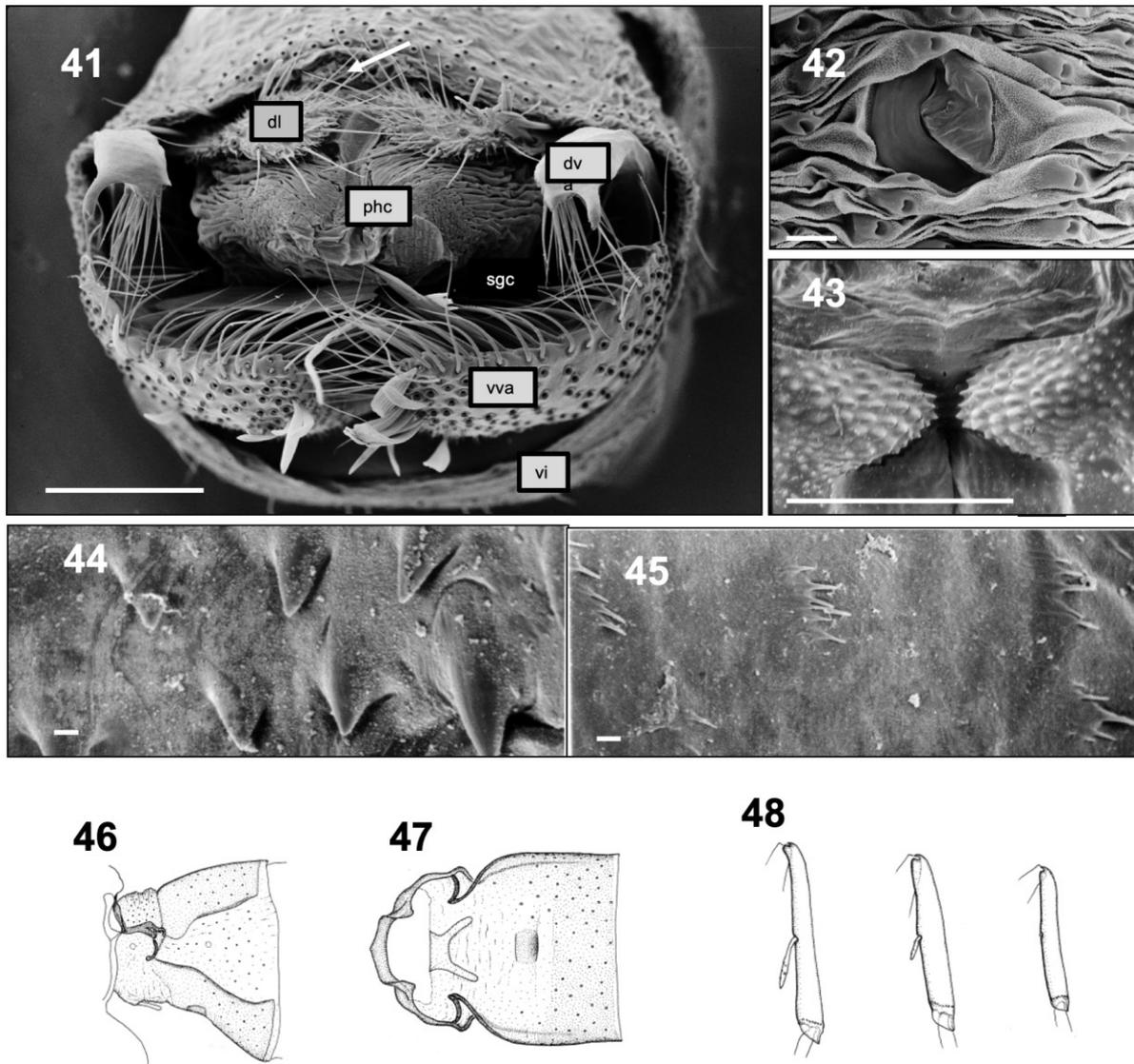
Figs 26–29. Structural details. Head (SEM): 26 anteroventral view of descaled head capsule of *Mnesarchella acuta*, showing compound eyes, reduced labrum, coiled tongue, large labial palps and small maxillary palps with vestigial mandibles; 27 fully scaled head of *Mnesarchaea paracosma*, with labial palps below; 28 outer margin of compound eye, *M. acuta*, showing part of the marginal comb of ribbed setae; 29 LH mandible of *M. acuta*. Abbreviations: ga—galea; la—labrum; lp—labial palp; md—mandible; mp—maxillary palp. Scale-line 0.1 mm.



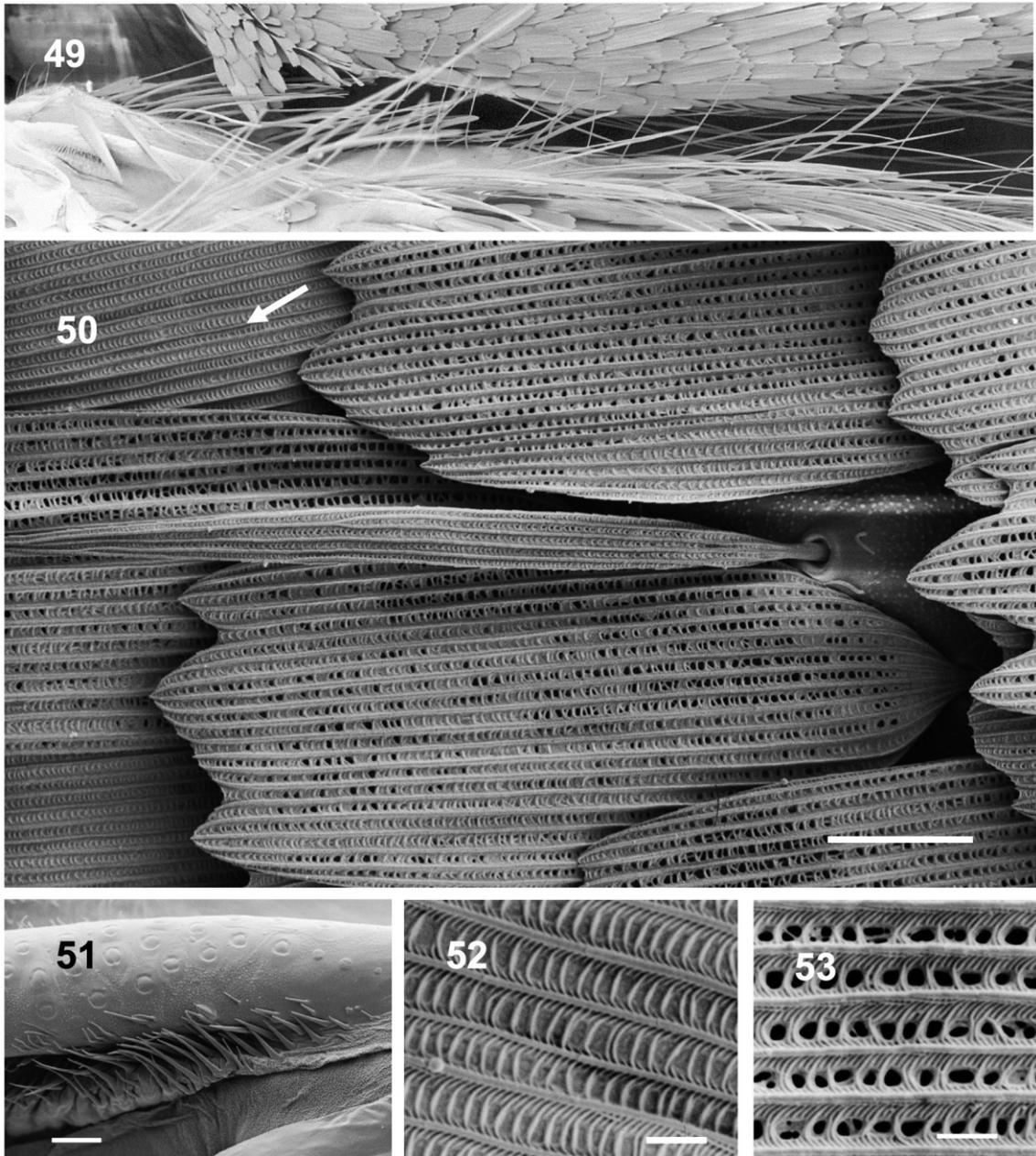
Figs 30–35. Antennal and palp details (SEM): 30 flagellomere of *Mnesarchella acuta* showing detail of rugose surface sculpturing; 31 *Mnesarchaea hudsoni* showing outer scale vestiture; 32 *M. acuta* a mid-length flagellomere showing unbranched multiporous sensilla (both thick (arrow) and thin) and scattered bases of overlying scales; 33 a mid-length flagellomere of *Mnesarchaea paracosma*, showing multibranching multiporous sensilla and scale bases concentrated towards proximal end of flagellomere; 34 terminal labial palp segment of *M. paracosma* with subapical vom Rath's organ (arrow); 35 detail of vom Rath's organ, *M. acuta*. Figs 32–34—scale-lines 0.01 mm; Fig. 35—0.001 mm.



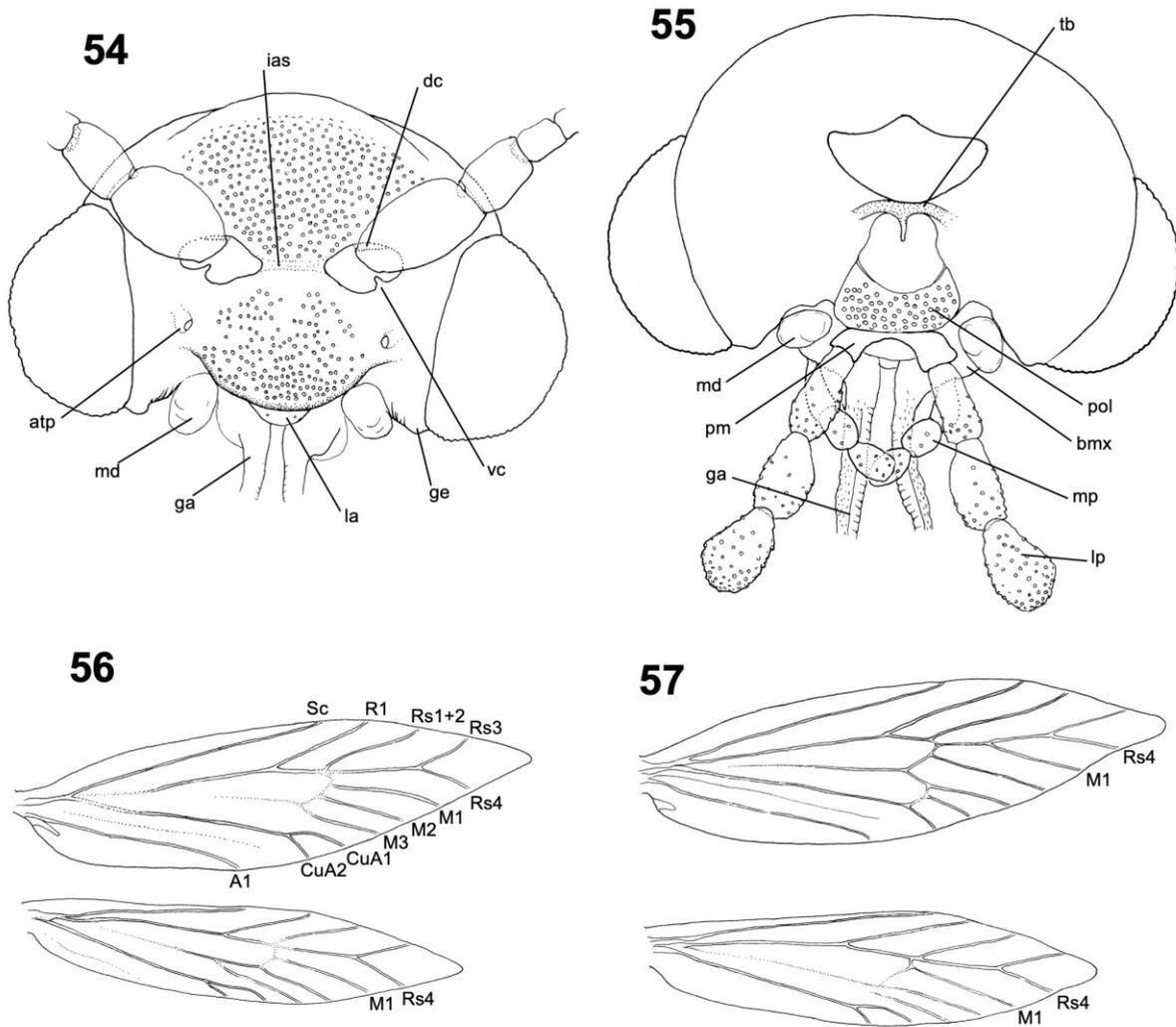
Figs 36–40. Structural details from serial microscope sections (slides in NZAC): 36 *Mnesarchaea paracosma*, TS head at level of mandibles showing mouthparts, sitophore and salivary duct. Slide Mn 553; 37 *Mnesarchella acuta*, median LS of head showing galea, salivary glands and orifice, ligula, sitophore and pharynx. Slide Mn 39; 38 *Mnesarchaea fallax*, LS male genital capsule showing anus and anal cone, phallus and phallocrypt, subanal periphallic arm, glandular area in roof of pseudoteguminal plate, reflexed portions of the valve arms and vinculum. Slide Mn 58; 39 *Mnesarchella fusilella*, TS male genital capsule at level of pseudoteguminal glandular area, showing trulleum sclerotisations and pecten, phallic complex, anus. Slide Mn 6; 40 *Mnesarchella falcata*, LS male genital capsule to show anus, subanal periphallic arm, phallic complex, vinculum. Slide Mn 56. Abbreviations: ac—anal cone; an—anus; br—brain; cib—cibarium; dva—dorsal valve arm; fg—frontal ganglion; ga—galea; ge—gena; gl—glandular area of pseudoteguminal plate; lig—ligula; lp—labial palp; md—mandible; mgn2—muscle inserted on vinculum; mp—maxillary palp; pe—pecten; ph—phallus; phc—phallocrypt; phy—pharynx; pls—postlabial sclerite; ptp—pseudoteguminal plate; sd—salivary duct; sgc—subgenital crypt; sit, st—sitophore; so—salivary orifice; sog—suboesophageal ganglion; spa—subanal periphallic arm; tbr—trulleum bridge; tl—tergal lobe of male segment 10; tr—trulleum sclerotisation; vi—vinculum; vva—ventral valve arm.



Figs 41–45. Male and female genitalia details, *Mnesarchella acuta* (SEM): 41 descaled abdomen of male, terminal view, showing anal cone (white arrow), setose dorsal A10 lobes, phallocrypt, distal ends of dorsal and ventral valve arms, vinculum; 42 abdominal spiracle of male; 43 sclerotized trulleum bar of male; 44 melanised scutes along V-sclerite 'bridge' which crosses roof of antrum, female; 45 small scutes on floor of antrum, female. **Figs 46–48.** Details of thorax and abdominal base: 46 lateral view of thoraco-abdominal region of *Mnesarchella hamadelpha*, showing free arms of sternite 1; 47 ditto in ventral view; 48 variable development of foretibial epiphysis between species: left *Mnesarchaea fallax*, centre *Mnesarchella acuta*, right *Mnesarchaea hudsoni*. Abbreviations: *di*—dorsal lobe of male segment A10; *dva*—dorsal valve arm; *phc*—phallocrypt; *sgc*—subgenital crypt; *vi*—vinculum; *vva*—ventral valve arm. Scale-lines: Fig. 41: 0.1 mm; Fig. 42: 0.01 mm; Figs 43, 44, 45: 0.1 mm.



Figs 49–53. Wing vestiture details (SEM): 49 photo montage of *Mnesarchella acuta* wings, showing scale morphology along overlap zone on dorsal side. Note flat scales cladding the jugal lobe (top left) and along anal margin of forewing (above); costal margin of hindwing (below) with numerous long piliform scales; 50 dorsal surface of forewing of *Mnesarchaea paracosma* near base of cell, showing outer hollow scales overlying inner solid ground scales (arrow) with a piliform scale in centre; 51 base of forewing radial vein of *M. paracosma*, ventral, with chordotonal sensilla; 52 solid scale detail, *M. paracosma*; 53 hollow scale detail, *M. acuta*. Scale lines: Fig 50: 0.1 mm; Fig 51: 0.01 mm; Figs 52, 53: 0.001 mm.



Figs 54–57. Head detail and wing venation: 54 *Mnesarchella acuta*, Scott's Beach NN, head capsule anterior, showing areas occupied by scale bases. 55 *M. acuta*, head capsule, posterior, with mouthparts; 56 *Mnesarchaea fallax*, Lewis Pass, wing venation with independent Rs3+4 and M1 in forewing; 57 *M. acuta*, Ohau Valley WN, wing venation with stalked Rs3+4 and M1 in forewing. Abbreviations: atp—anterior tentorial pit; bm—basal maxilla; dc—dorsal anterior condyle of antennal socket; ga—galea; ge—gena; ias—inter-antennal sulcus; la—labrum; lp—labial palp; md—mandible; mp—maxillary palp; pm—prementum (or prelabium); pol—postlabial sclerite; prl—prelabium (or 'prementum'); tb—tentorial bridge; vc—ventral condyle of antennal socket.

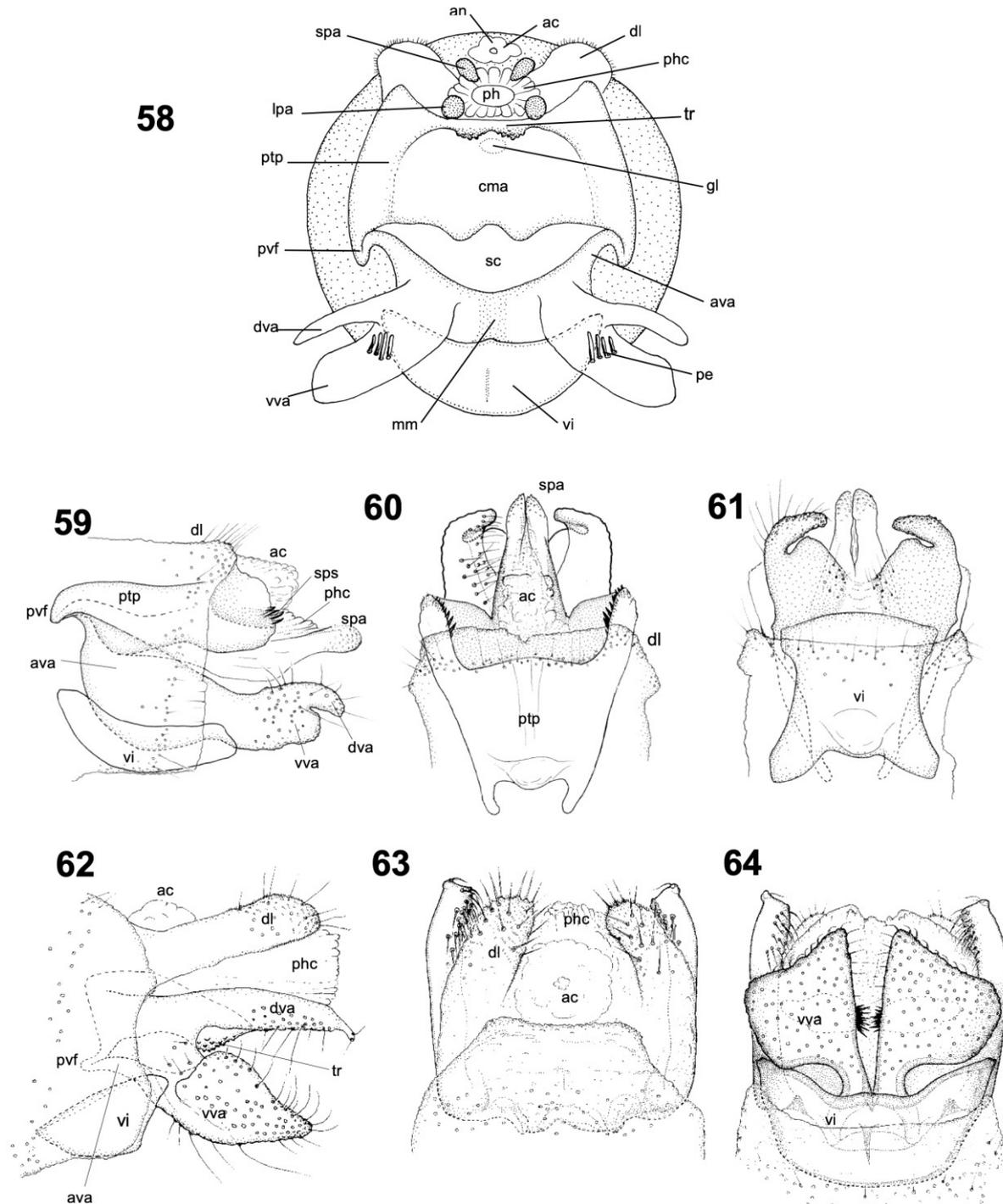
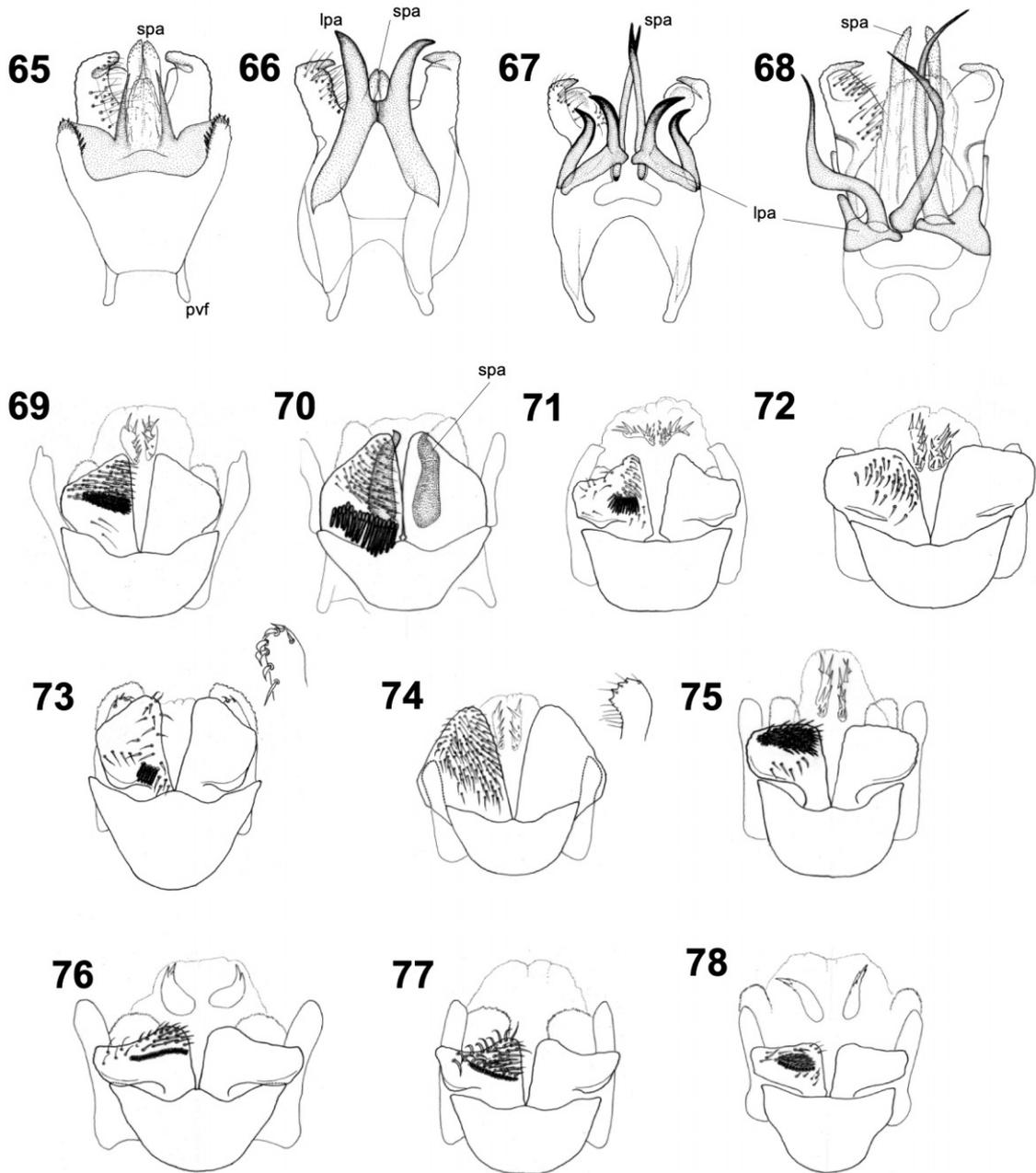
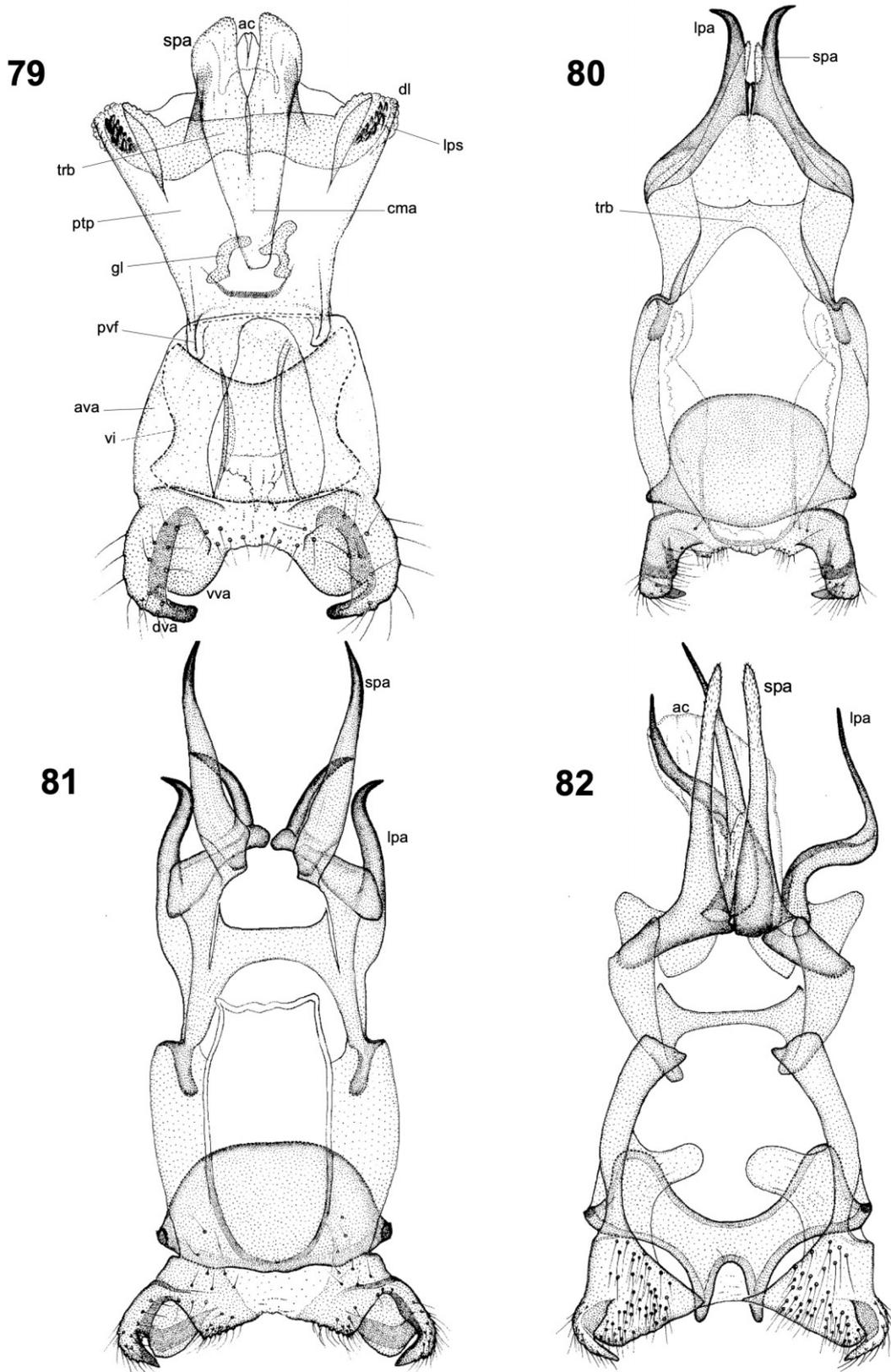


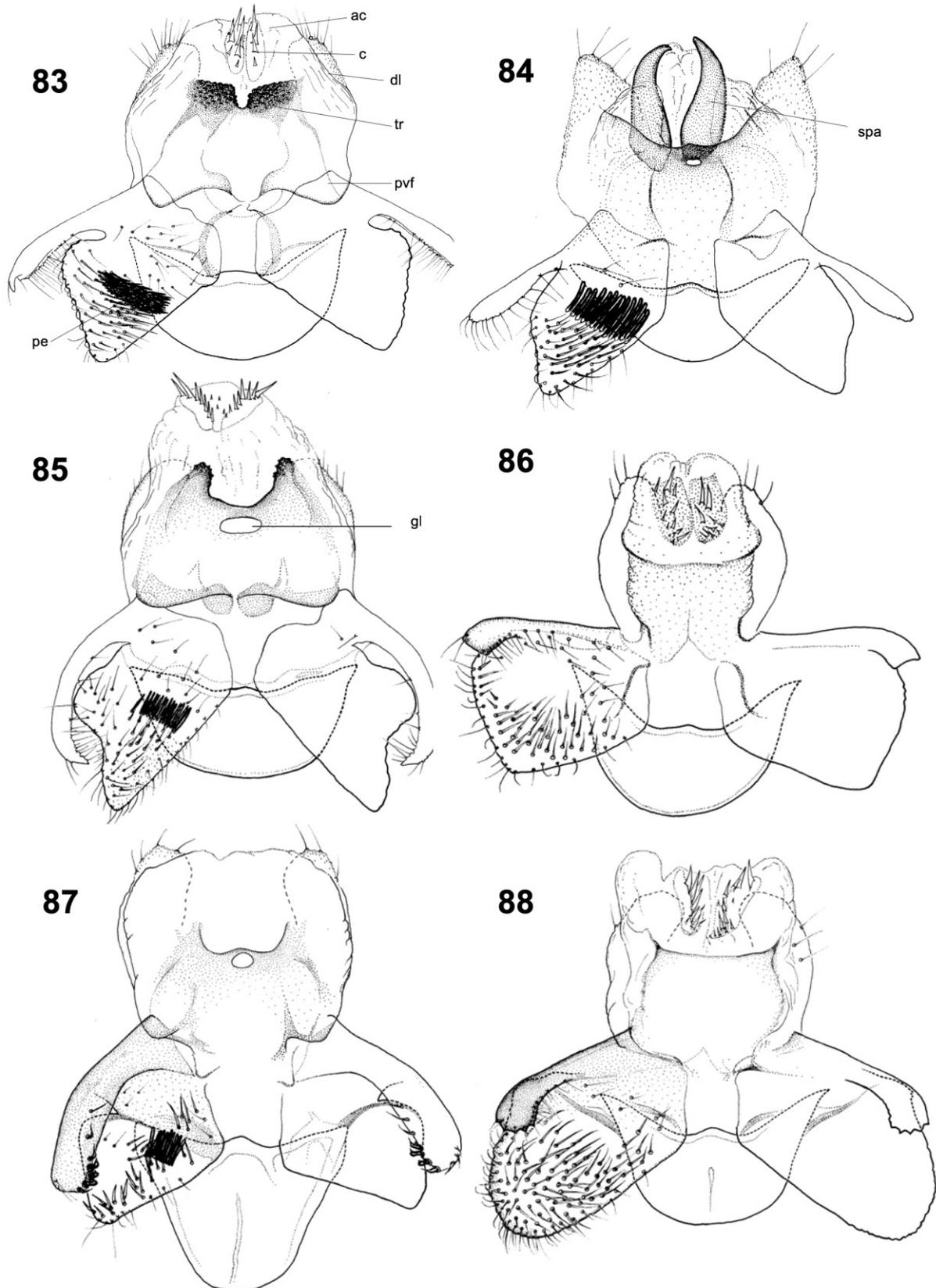
Fig 58. Diagram to explain male genitalia terminology as viewed in a conventional 'opened' taxonomic preparation. The preparation is hinged open at the points marked pvf (points of pseudoteguminal plate and valve fusion). **Figs 59–64.** Terms explained in relation to the two genera: 59 *Mnesarchaea fallax*, lateral view; 60 *M. fallax*, dorsal view; 61 *M. fallax*, ventral view; 62 *Mnesarchella acuta*, lateral view; 63 *M. acuta*, dorsal view; 64 *M. acuta*, ventral view. Abbreviations: ac—anal cone; an—anus; ava—anterior valve arm (internal); cma—central membranous area; dl—dorsal lobe of segment 10; dva—dorsal valve arm; gl—glandular area of pseudoteguminal plate; lpa—lateral periphallic arm; mm—mid-ventral membranous area of male valve; pe—pecten; ph—phallus; phc—phallocrypt; ptp—pseudoteguminal plate; pvf—pseudoteguminal plate-valve fusion point; sc—sub-genital crypt; spa—subanal periphallic arm; tr—trulleum sclerotisation; vi—vinculum; vva—ventral valve arm.



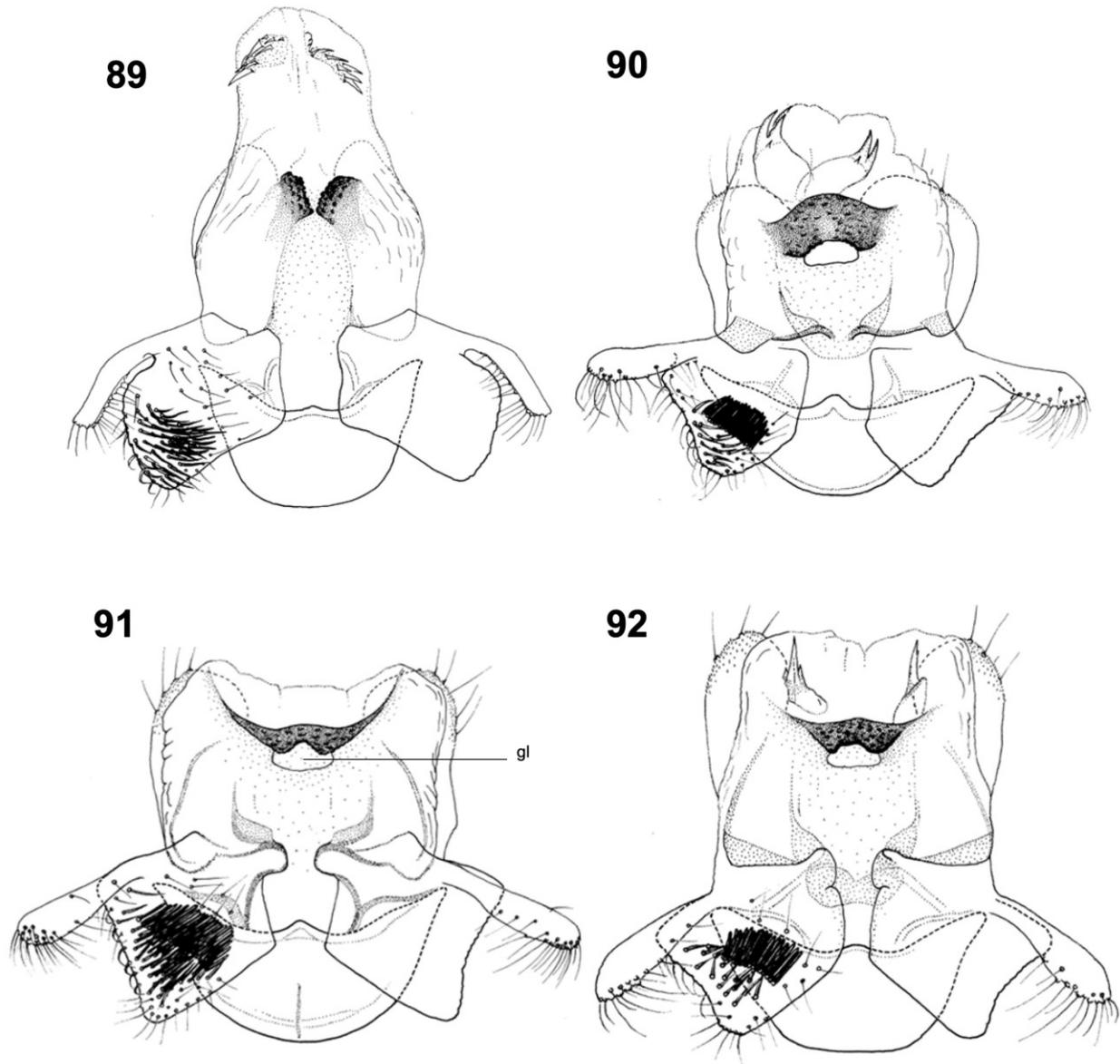
Figs 65–78. Male genitalia of all species illustrated after maceration and clearing, but otherwise left in situ. To be used in conjunction with the key as an aid to rapid identification. (65–68) *Mnesarchaea* species in dorsal view: 65 *M. fallax*; 66 *M. fusca*; 67 *M. hudsoni*; 68 *M. paracosma*. (69–78) *Mnesarchella* species in ventral view: 69 *M. acuta*; 70 *M. falcata*; 71 *M. hamadelpha*; 72 *M. ngahuru*; 73 *M. philpotti*; 74 *M. stellae*; 75 *M. vulcanica*. 76 *M. dugdalei*; 77 *M. fusilella*; 78 *M. loxoscia*. Abbreviations: lpa—lateral periphallitic arm; pvf—pseudoteguminal plate—valve fusion point; spa—subanal periphallitic arm.



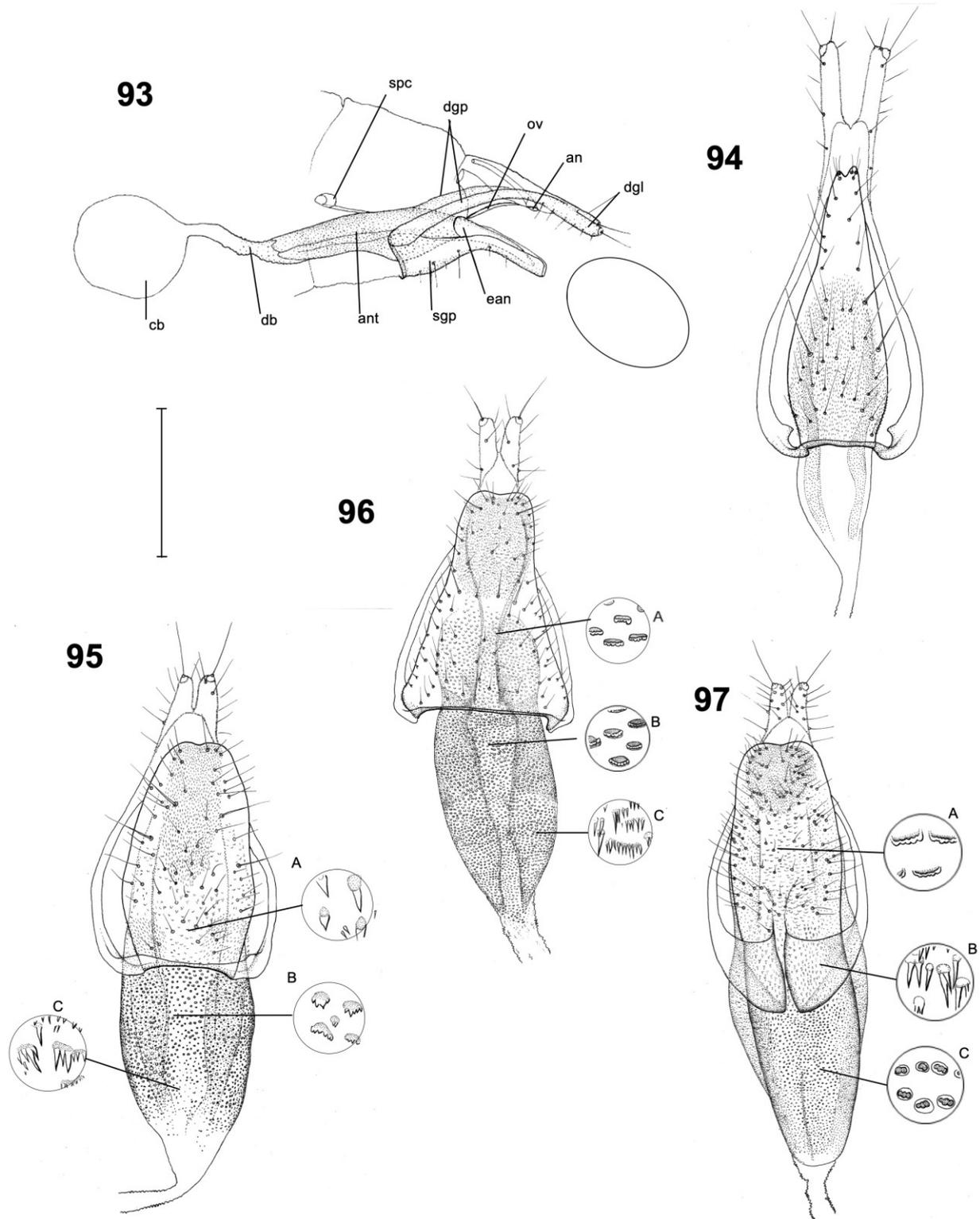
Figs 79–82. Male genitalia of *Mnesarchaea* species, 'opened' at pseudoteguminal/valve fusion points to reveal characters of taxonomic value: 79 *Mnesarchaea fallax*, Canaan, Takaka Hill, NN (slide G448); 80 *M. fusca*, Waitohi Valley, SD (slide G430); 81 *M. hudsoni*, Wilton's Bush, WN (paratype slide G458); 82 *M. paracosma*, Glacier Burn, OL (slide G437). Abbreviations: *ac*—anal cone; *ava*—anterior valve arm (internal); *cma*—central membranous area of pseudoteguminal plate; *dl*—dorsal lobe of segment 10; *dva*—dorsal arm of valve; *gl*—glandular area of pseudoteguminal plate; *lpa*—lateral periphalllic arm; *lps*—lateral pseudoteguminal spine patch; *ptp*—pseudoteguminal plate; *pvf*—pseudoteguminal plate-valve fusion point; *spa*—subanal periphalllic arm; *tl*—tergal lobe of segment A 10; *trb*—trulleum bridge; *vi*—vinculum; *vva*—ventral valve arm.



Figs 83–92. Male genitalia of *Mnesarchella* species, opened at pseudoteguminal/valve fusion points to reveal characters of taxonomic value: (83–88) 83 *Mnesarchella acuta*, Orongorongo Valley, WN (slide G217); 84 *M. falcata*, Ohakune Ranger Station, Mangawhero Stream, TO (paratype slide G522); 85 *M. hamadelpha*, Karamea, NN (slide G274); 86 *M. ngahuru*, Manuoha, GB (paratype slide G334); 87 *M. philpotti*, McKinnon Pass, FD (paratype slide G524 AMNZ); 88 *M. stellae*, U. Mohikinui Valley, NN (paratype slide G523); Abbreviations: ac—anal cone, c—cornuti; dl—dorsal lobe of segment 10; gl—glandular area of pseudoteguminal plate; pvf—pseudoteguminal plate/valve fusion point; spa—subanal periphallitic arm; tl—tergal lobe of segment A10; tr—trullium sclerotisation.



(89–92) 89 *M. vulcanica*, Pouakai Range, TK (paratype slide G313); 90 *M. dugdalei*, Fairy Falls, AK (paratype slide G417); 91 *M. fusilella*, Lake Okataina, BP (slide G402); 92 *M. loxoscia*, Table Mountain, Kauaeranga Valley, CL (slide G368).



Figs 93–97. Female genitalia of *Mnesarchaea* species (93 lateral view; 94–97 ventral views). 93 diagram of terminology used on female genitalia, including egg outline to scale. 94 *Mnesarchaea fallax*, Hauhangatahi, TO; 95 *M. fusca*, Waitohi Valley, SD; 96 *M. hudsoni*, Otaki Forks, WN (genitalia vial G454); 97 *M. paracosma*, Princhester Ck, SD. Abbreviations: an—anus; ant—antrum; cb—corpus bursae; db—ductus bursae; dgl—dorsal lobes of genital plate; dgp—dorsal genital plate; ean—entrance to antrum; ov—ovipore; sgp—subgenital plate; spc—spermatheca. Scale-line 0.3 mm.

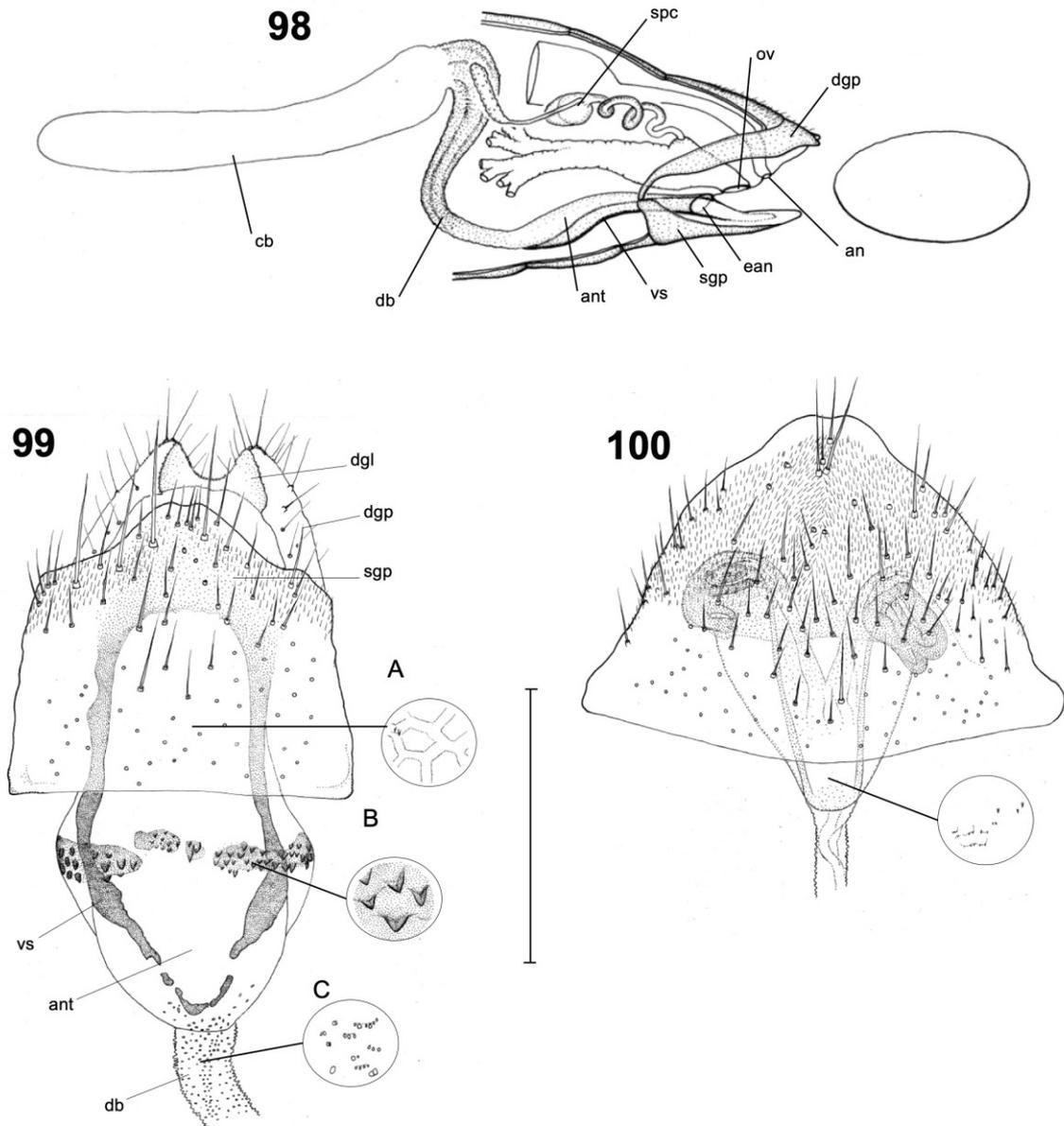
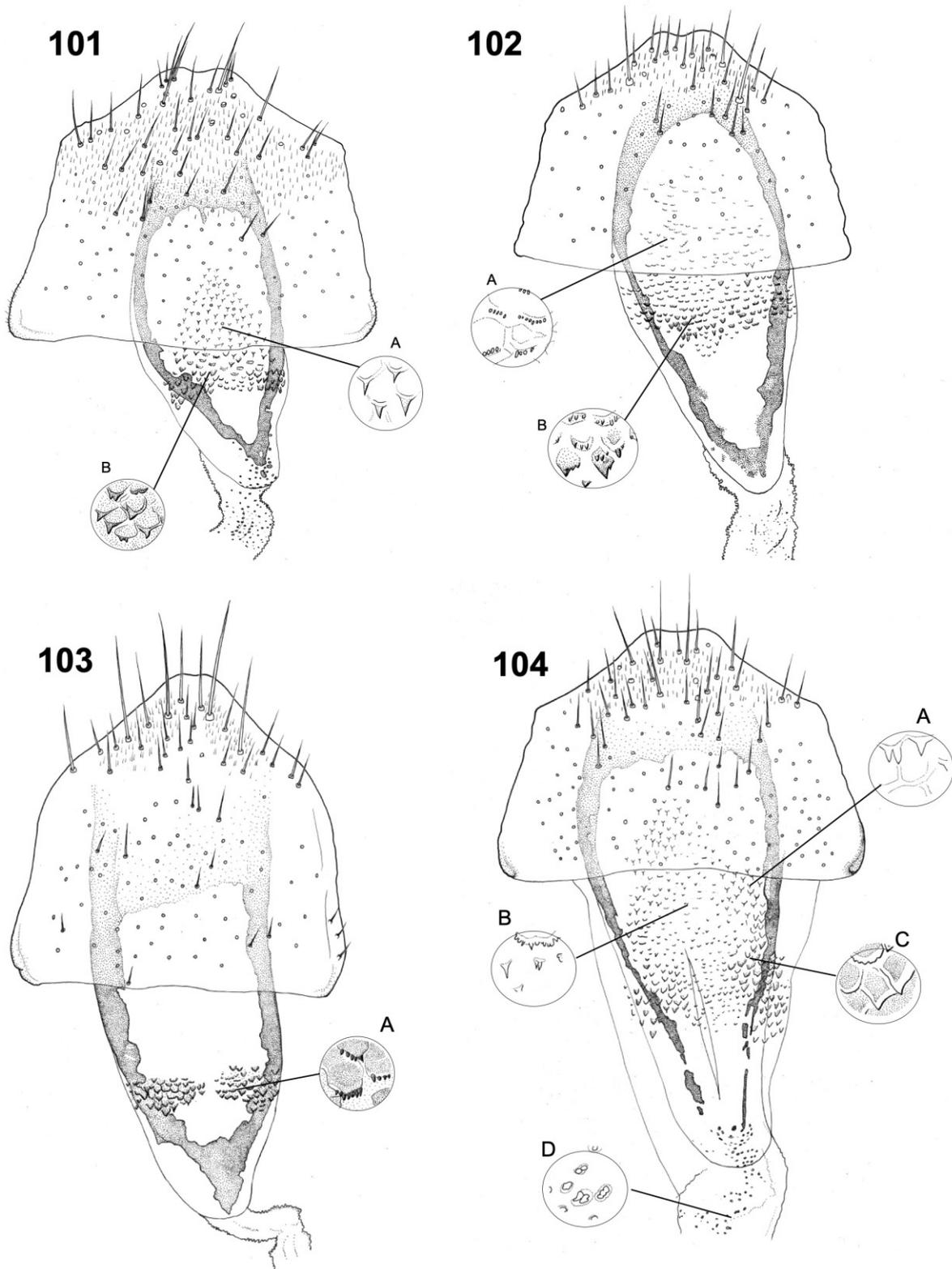
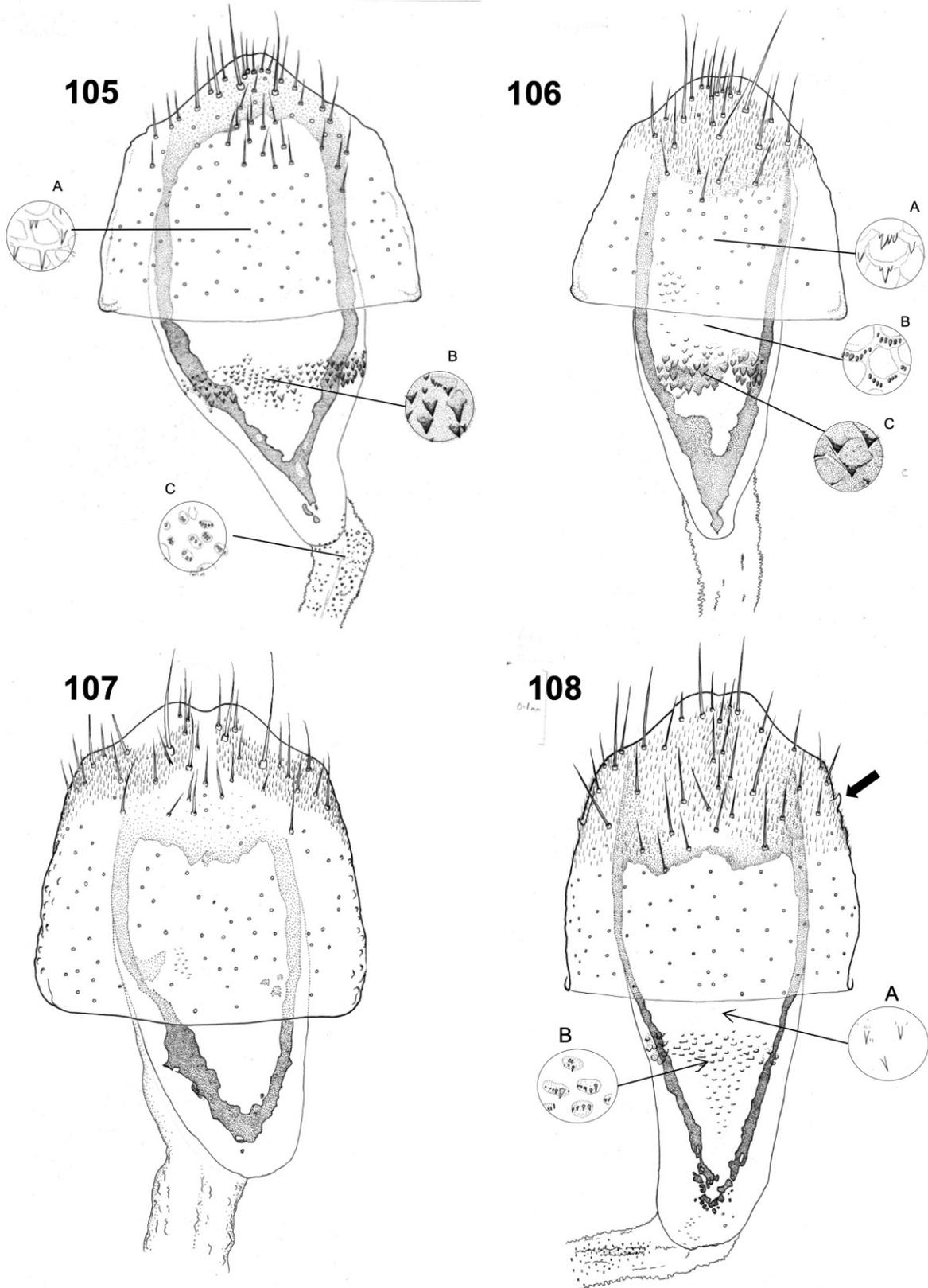


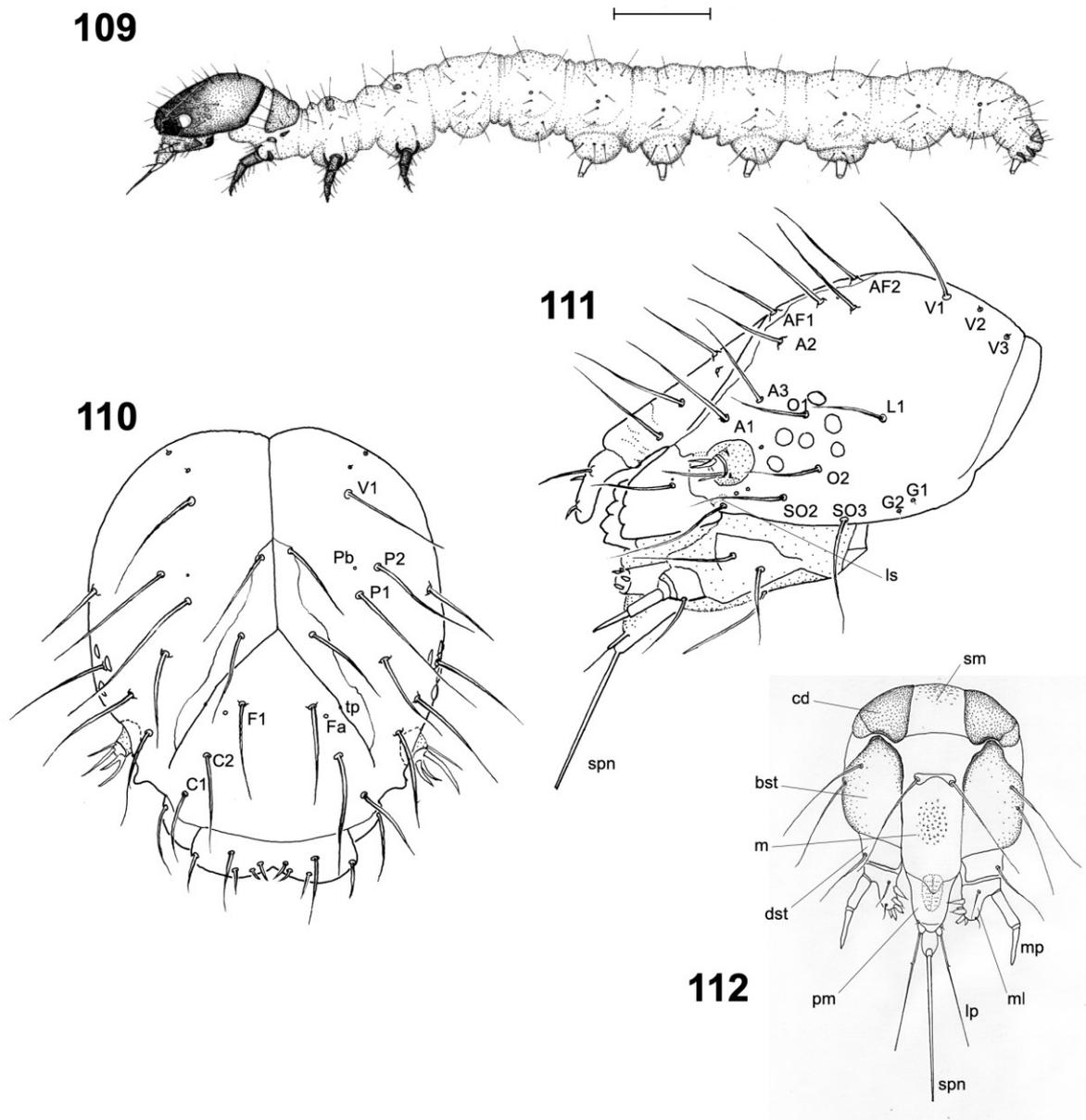
Fig. 98–108. Female genitalia of *Mnesarchella* species. 98 diagram in lateral view to show terminology, including egg outline to scale. (Figs 99–108 ventral views. Note that Figs 100–108 omit the dorsal genital plate): 99 *M. acuta*, Copeland Valley, WD, showing both dorsal and subgenital plates, V-sclerite and antrum; 100 *M. falcata*, Waitanguru, WO; Abbreviations: an—anus; ant—antrum; cb—corpus bursae; db—ductus bursae; dgl—dorsal lobes of genital plate; dgp—dorsal genital plate; ean—entrance to antrum; ov—ovipore; sgp—subgenital plate; spc—spermathecal; vs—v-sclerite. Scale-line 0.3 mm.



(101–104) Female genitalia to scale: 101 *M. hamadelpha*, Mt Dundas, WN; 102 *M. ngahuru*, Ruapehu, TO; 103 *M. philpotti*, Percy Valley, FD; 104 *M. stellae*, U. Mohikinui Valley, NN. Scale-line 0.3 mm.

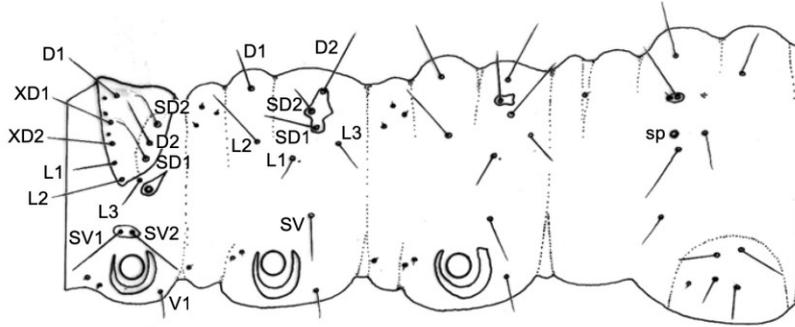


(105–108) Female genitalia to scale: 105 *M. vulcanica*, Waihothonu, TO. 106 *M. dugdalei*, Lake Rotopounamu, TO; 107 *M. fusilella*, Wilton's Bush, WN; 108 *M. loxoscia*, Moehau, CL. Scale-line 0.3 mm.

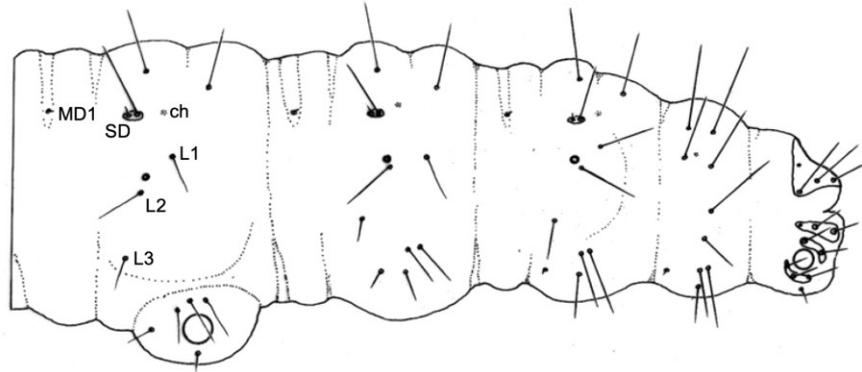


Figs 109–120. Immature stages. (109–112) Larval morphology and chaetotaxy, *Mnesarchella acuta*: 109 mature larva lateral view; 110 head capsule, anterior view; 111 head capsule, lateral view; 112 maxillolabial complex, ventral view. Abbreviations: bst—basistipes; cd—cardo; dst—dististipes; lp—labial palp; ls—lateral slit; m—mentum; ml—maxillary lobe; mp—maxillary palp; pm—prementum; sm—submentum; spn—spinneret. Scale-line 1 mm.

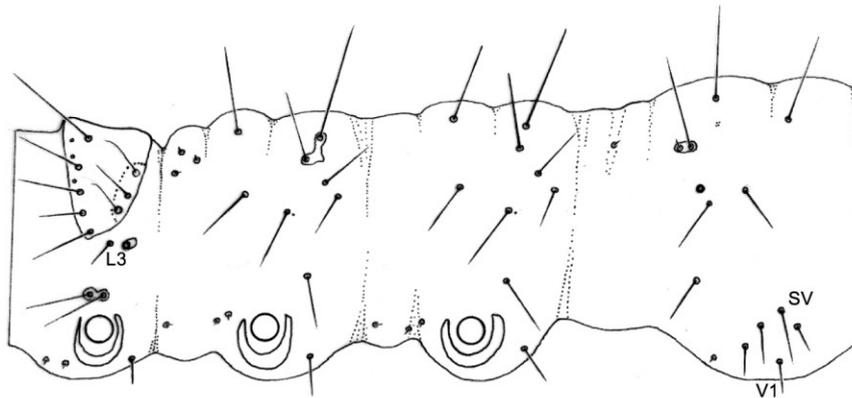
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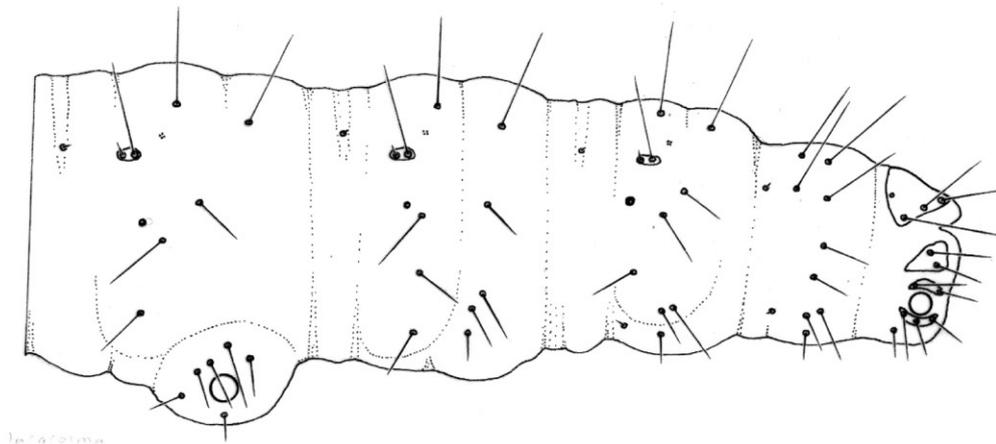
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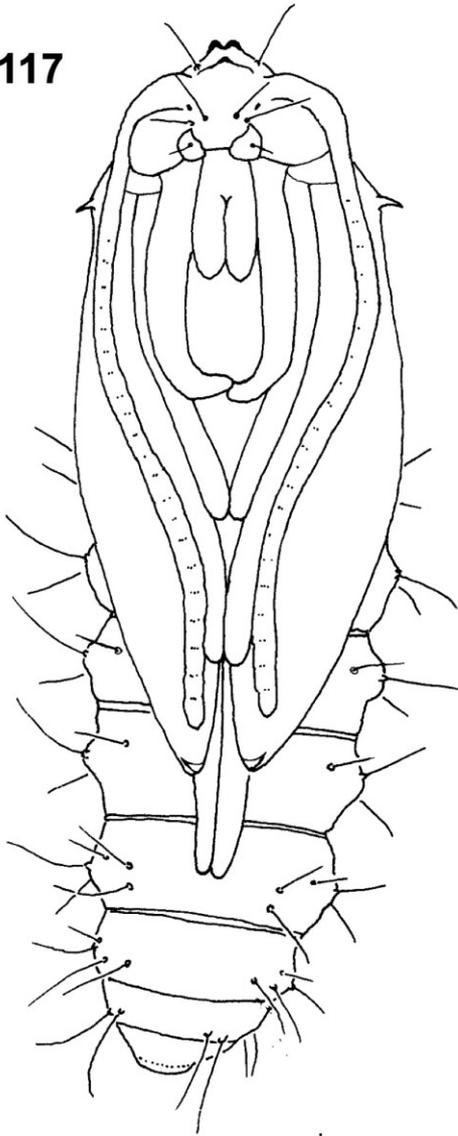
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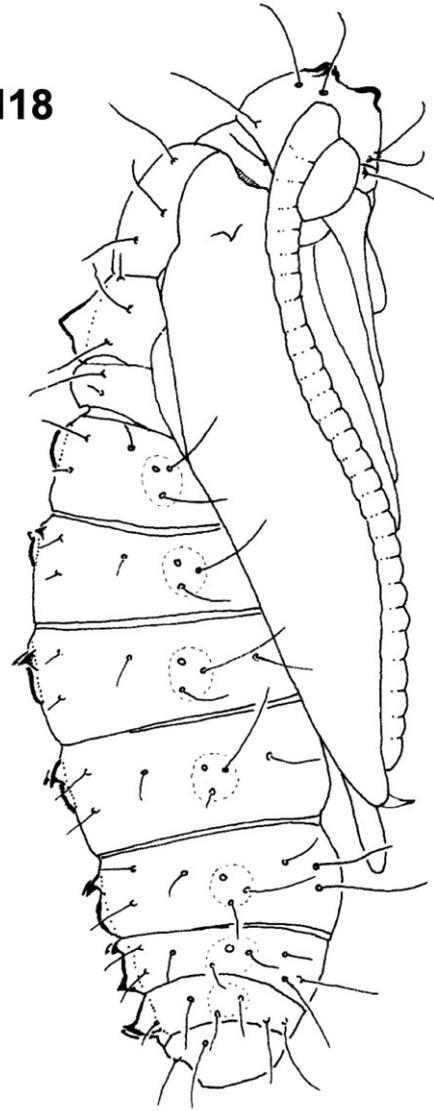
Mnesarchaea

(113–116) Trunk chaetotaxy: 113 *Mnesarchella acuta* segments T1–3, A1; 114 *M. acuta* segments A6–10; 115 *Mnesarchaea paracosma*, segments T1–3, A1; 116 *M. paracosma*, segments A6–10. Abbreviations: ch—chordotonal organ, sp—spiracle.

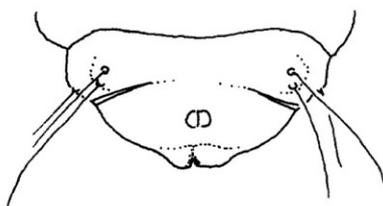
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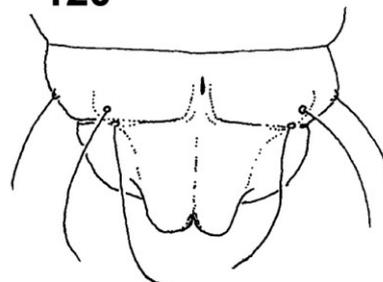
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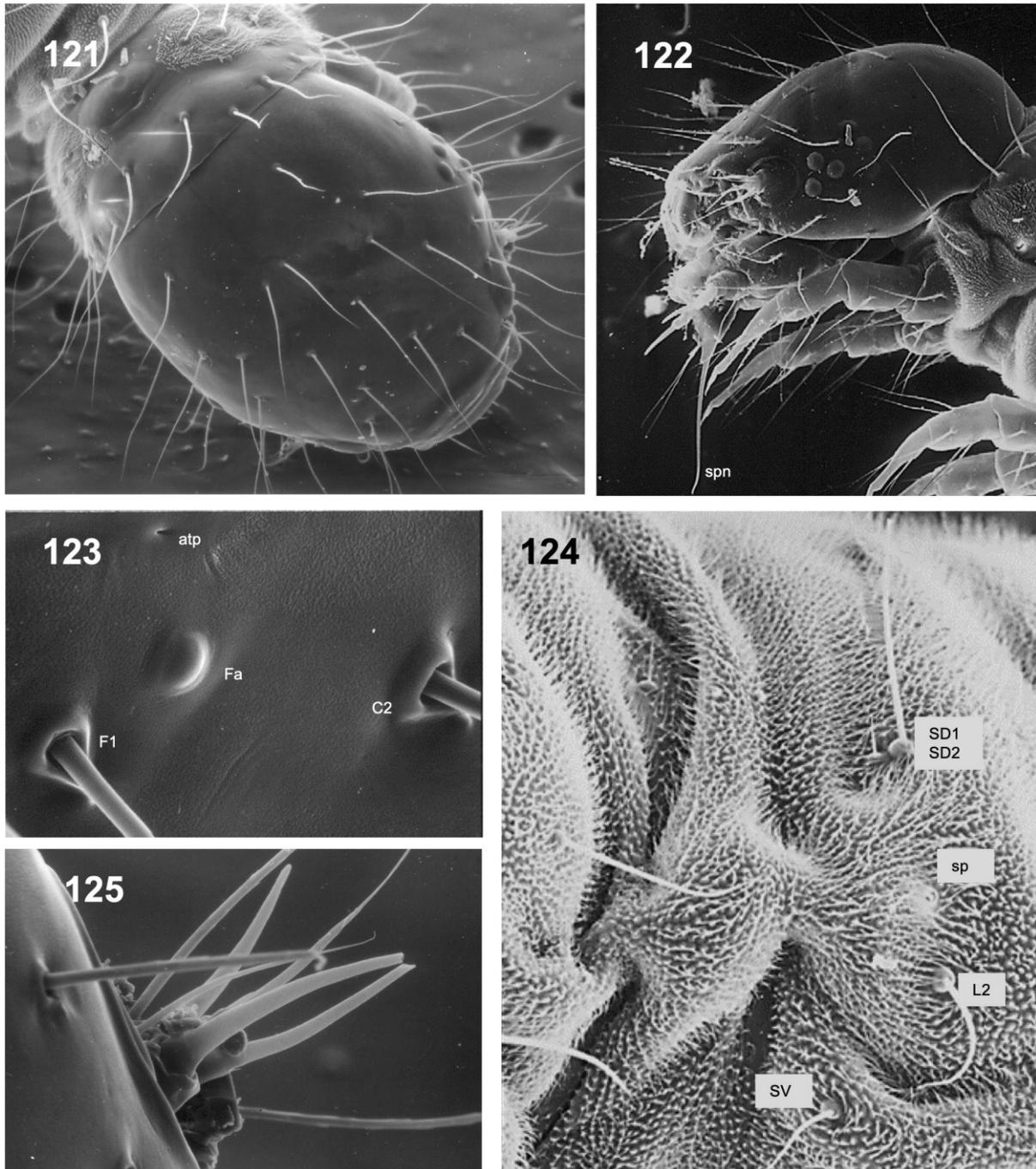
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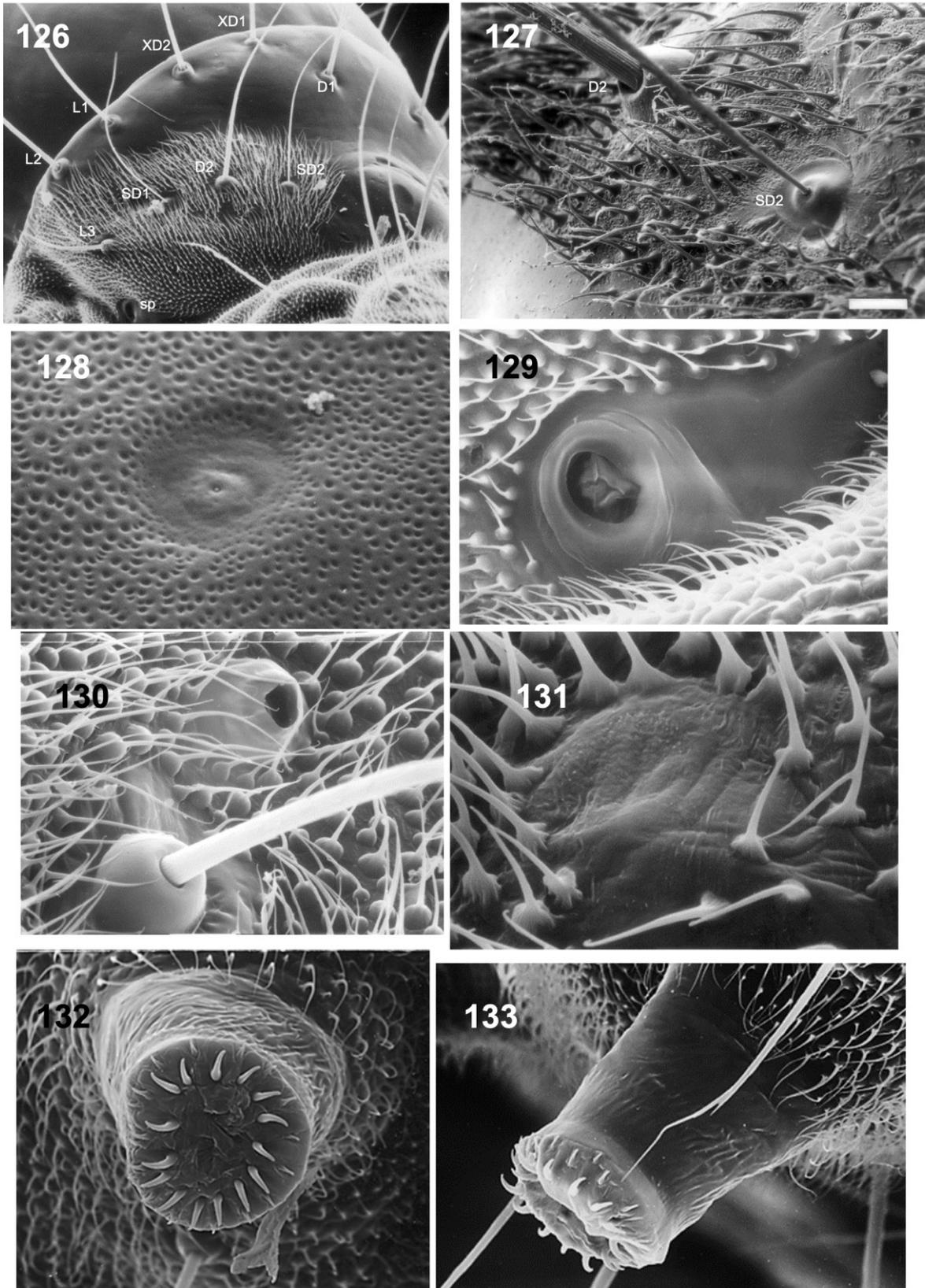
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(117–120) Pupa, *Mnesarchella acuta*: 117 ventral view; 118 lateral view; 119 male pupa, terminal segments, ventral; 120 female pupa, terminal segments ventral view.



Figs 121–133. Larval features, SEM: 121 head capsule of mature *Mnesarchella acuta*, antero-dorsal view; 122 Head capsule of mature *M. acuta* in lateral view; 123 anterior tentorial pit (top margin) with campaniform ‘puncture’ Fa between setae F1 and C2 below; 124 larval cuticle of *M. fusilella* on segment A1, showing microtrichia and region around spiracle in lateral view; 125 antenna, *M. fusilella*. Abbreviations: atp—anterior tentorial pit, sp—spiracle, spn—spinneret. Scale-line 0.01 mm.



(126–133) Larval features SEM: 126 Prothoracic shield, *Mnesarchella fusilella*, showing chaetotaxy; 127 third instar *M. acuta* larval setae D2 and SD2, on prothoracic shield, scale-line 0.01 mm; 128 ‘pit’ sensilla between XD1 and XD2 on prothoracic shield, *M. fusilella*; 129 prothoracic spiracle, *M. fusilella*; 130 L1 seta and spiracle on segment A1, *M. fusilella*; 131 chordotonal organ posterior to seta SD1 on segment A1 of *M. fusilella*; 132 planta with crotchets, larval proleg of *M. fusilella*; 133 lateral view proleg, *M. fusilella*.

Fig. 134. Seasonal occurrence of Mnesarchaeidae in New Zealand, based on museum collection records. The arrow bar shows range of capture dates, the broad bar represents approximately 80% of the records

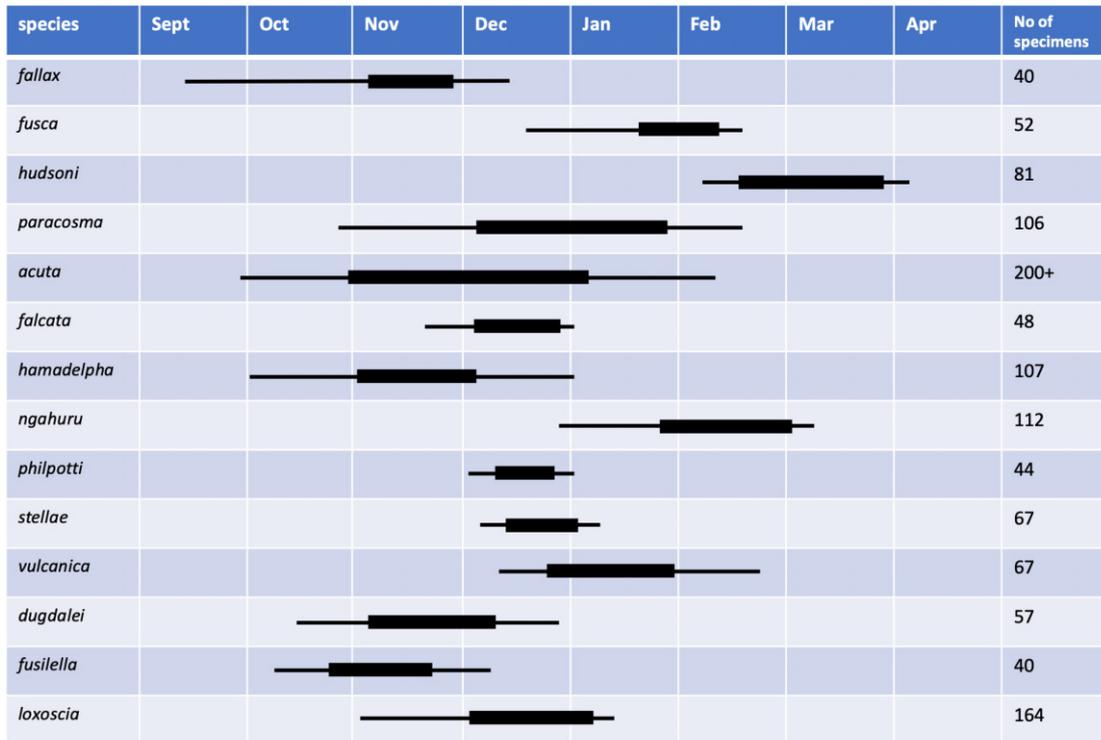


Fig. 134. Phenology of Mnesarchaeidae.

Fig. 135. Species relationships as determined from parsimony analysis of three portions of the mitochondrial genome from a sample of 17 specimens plus two hepialid outgroups. Two equally parsimonious trees resulted which agree on relationships. One is shown below. The two main clusters are strongly supported and now distinguished as genera. Three species form a minor subclade – *dugdalei*, *fusilella* and *loxoscia*. Species relationships within *Mnesarchella* have support and both trees agree on relationships but the number of synapomorphies is too low for statistical confirmation. (Numbers shown are the number of assigned character changes (synapomorphies))

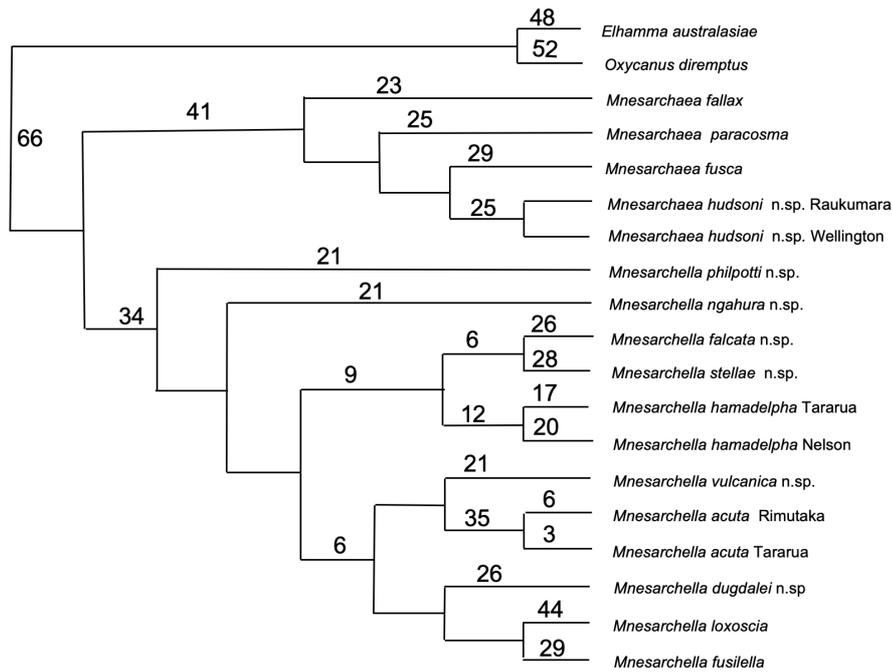
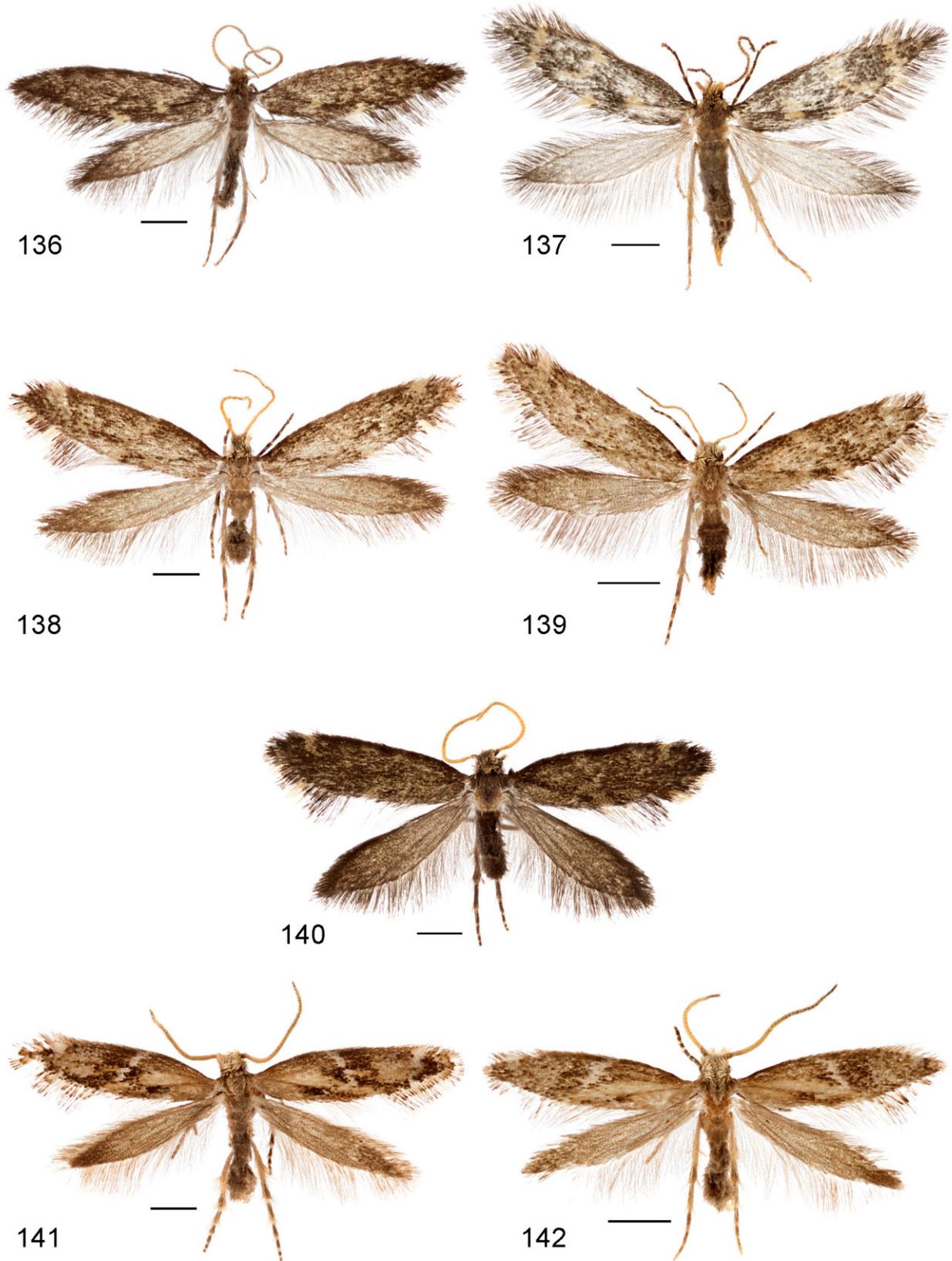
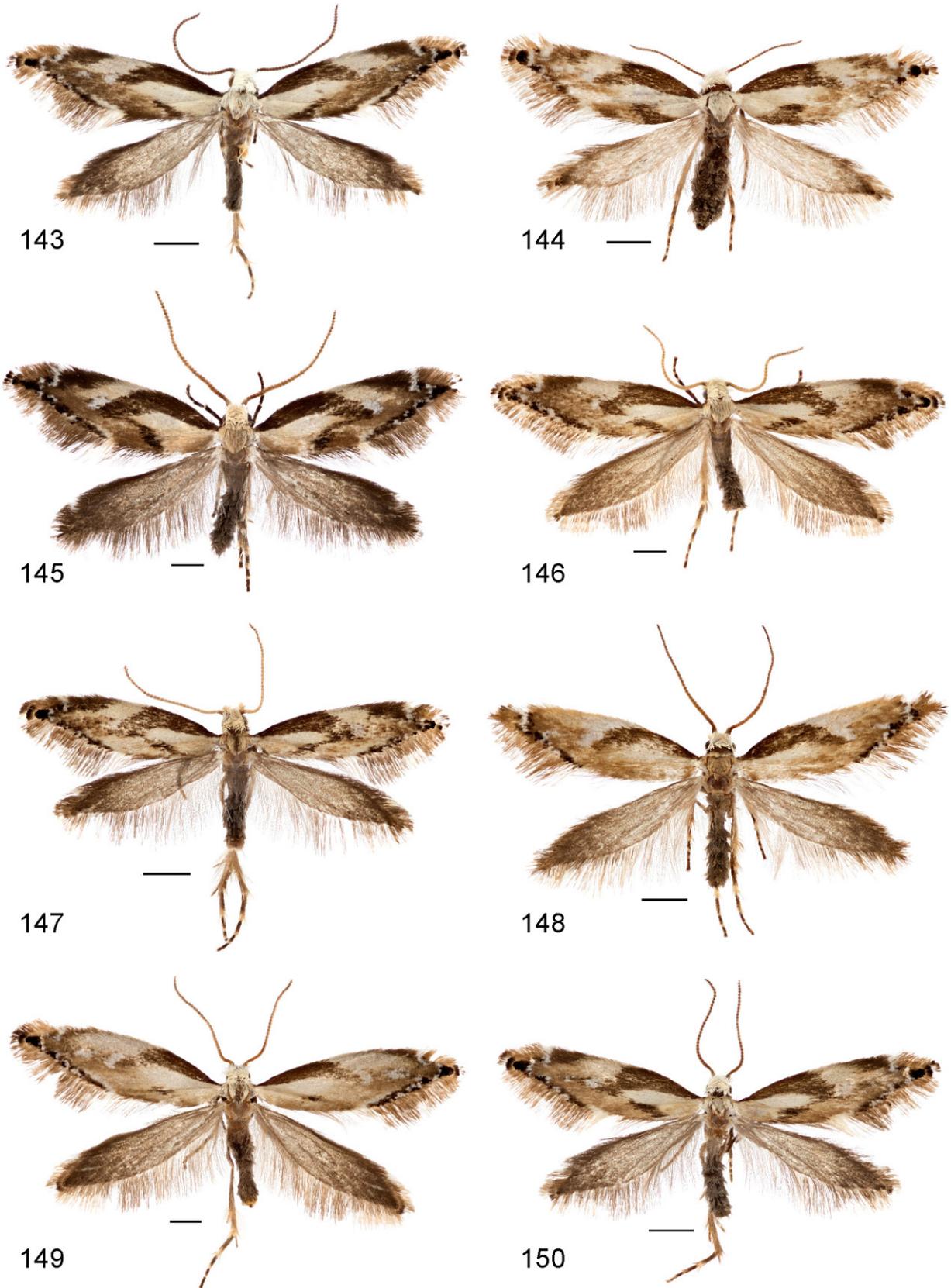


Fig. 135. A simplified phylogeny for species of Mnesarchaeidae.



Figs 136–156. Adults of *Mnesarchaea* and *Mnesarchella*. Specimens lodged in NZAC (photographed by Birgit E. Rhode). (136–150) *Mnesarchaea*: 136 male *M. fallax*; 137 female *M. fallax*; 138 male *M. fusca*; 139 female *M. fusca*; 140 male *M. hudsoni*; 141 *M. paracosma*; 142 female *M. paracosma*.



(143–150) *Mnesarchella* (*acuta*-group): 143 male *M. acuta*; 144 female *M. acuta*; 145 male *M. falcata*; 146 male *M. hamadelpha*; 147 male *M. ngahuru*; 148 HT male *M. philpotti*; 149 male *M. stellae*; 150 male *M. vulcanica*.



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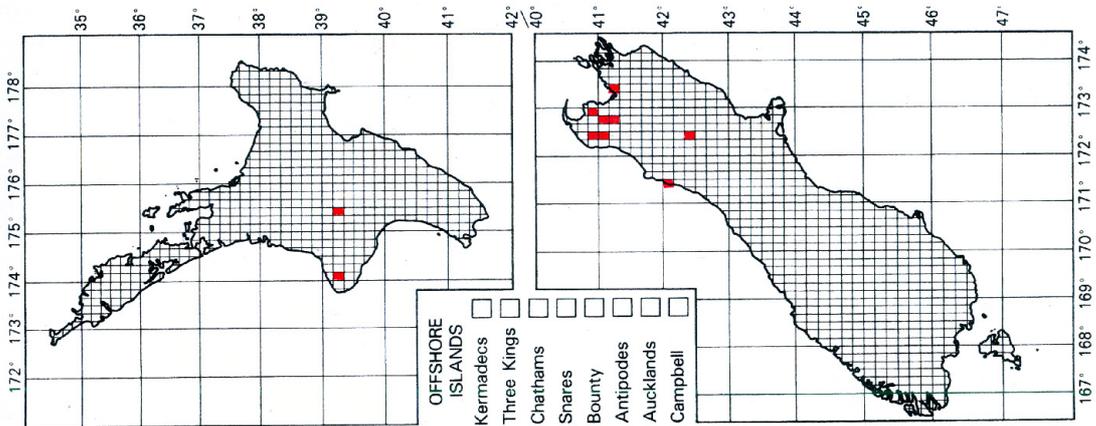


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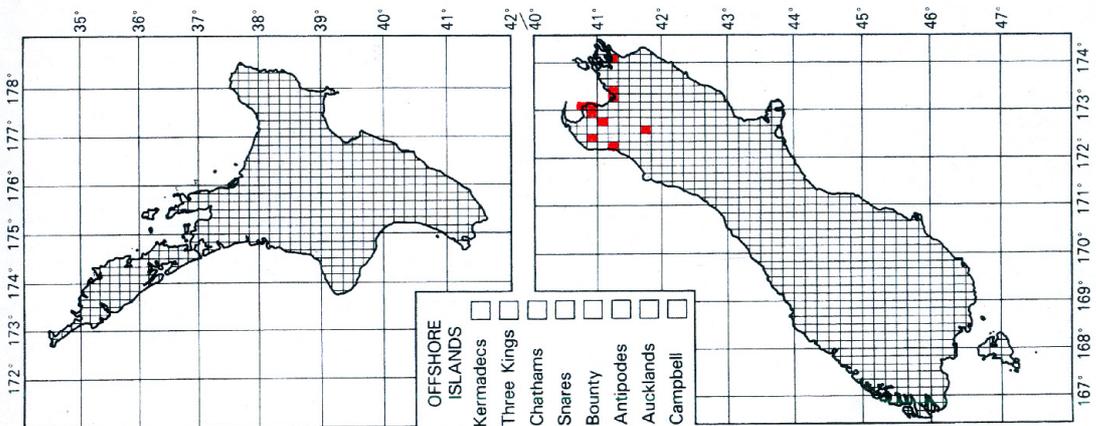


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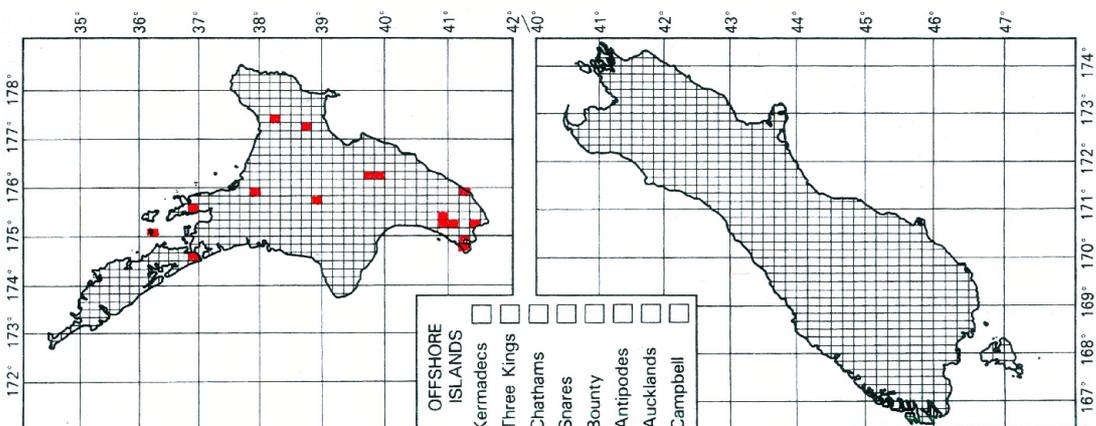
(151–156) *Mnesarchella* (*fusilella*-group): 151 male *M. dugdalei*; 152 female *M. dugdalei*; 153 male *M. fusilella*; 154 female *M. fusilella*; 155 male *M. loxoscia*; 156 female *M. loxoscia*.



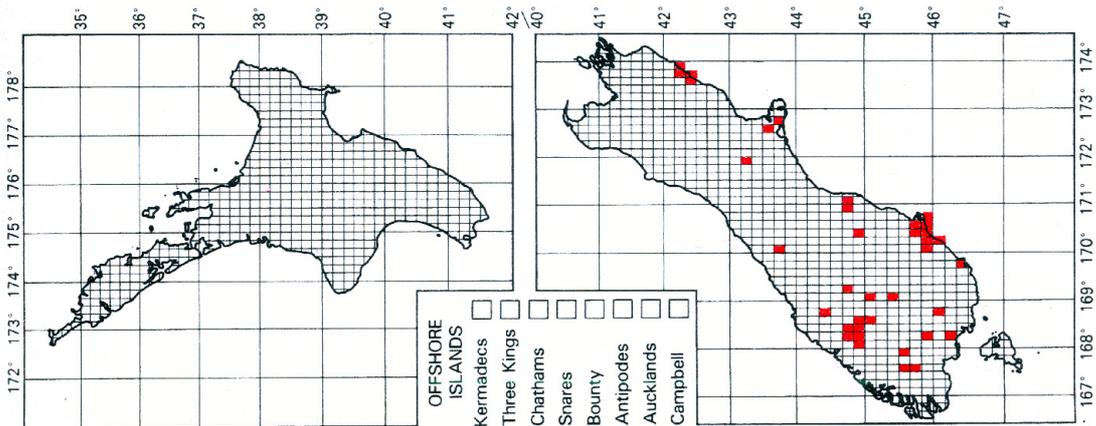
Map 1 *Mnesarchaea fallax*



Map 2 *M. fusca*

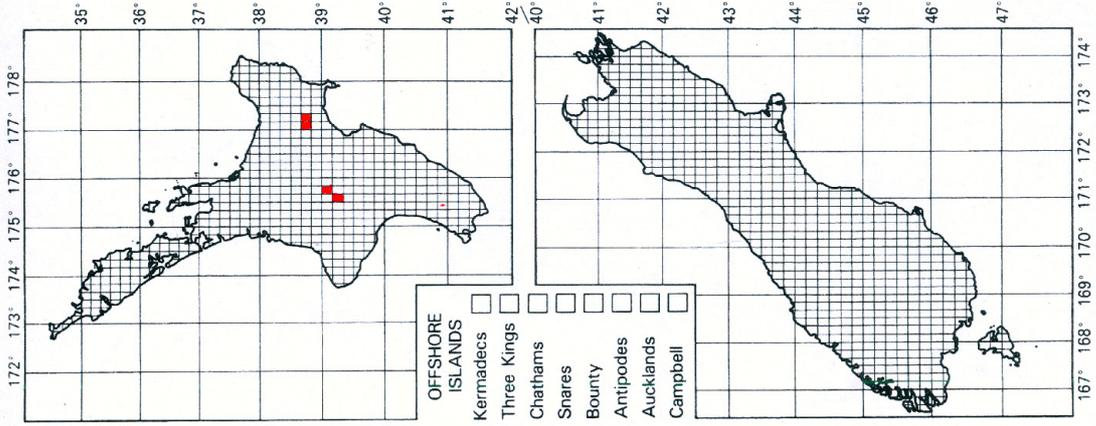


Map 3 *M. hudsoni*

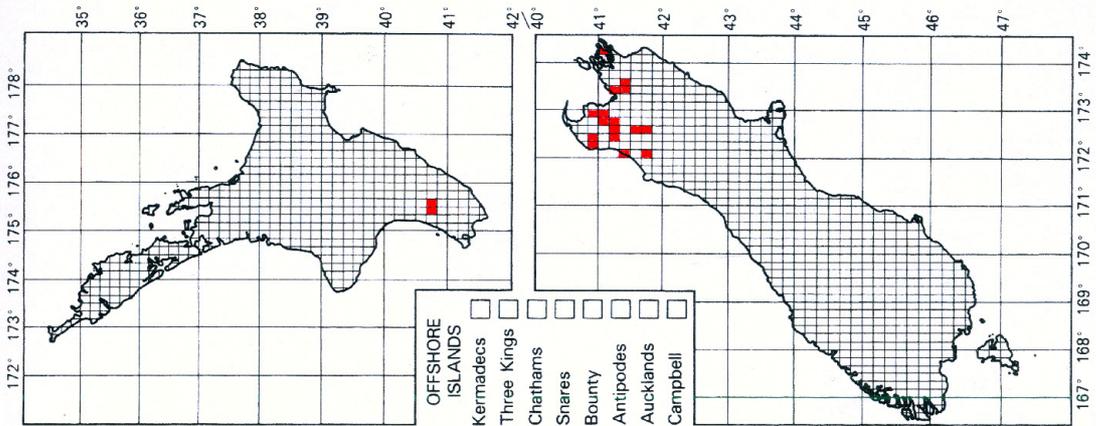


Map 4 *M. paracosma*

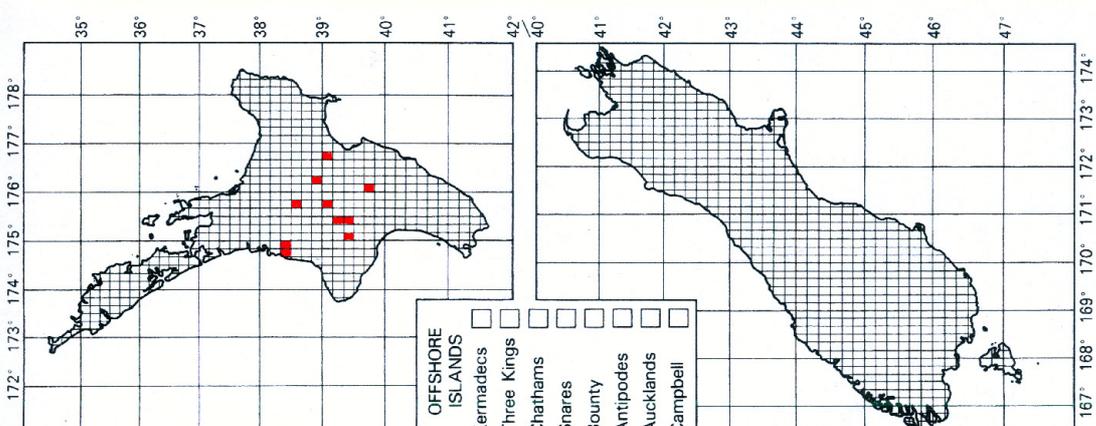
Species distribution maps according to the area codes of Crosby *et al.* (1976, 1988).



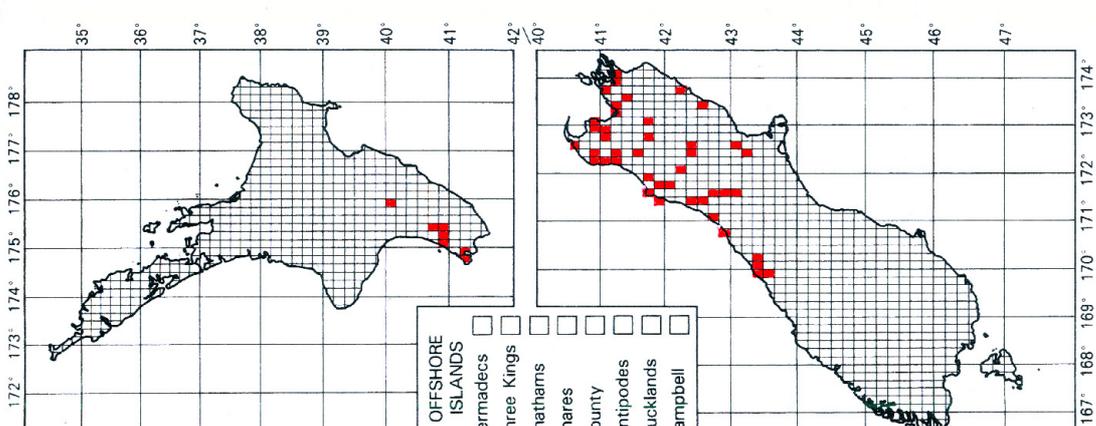
Map 5 *Mnesarchella acuta*



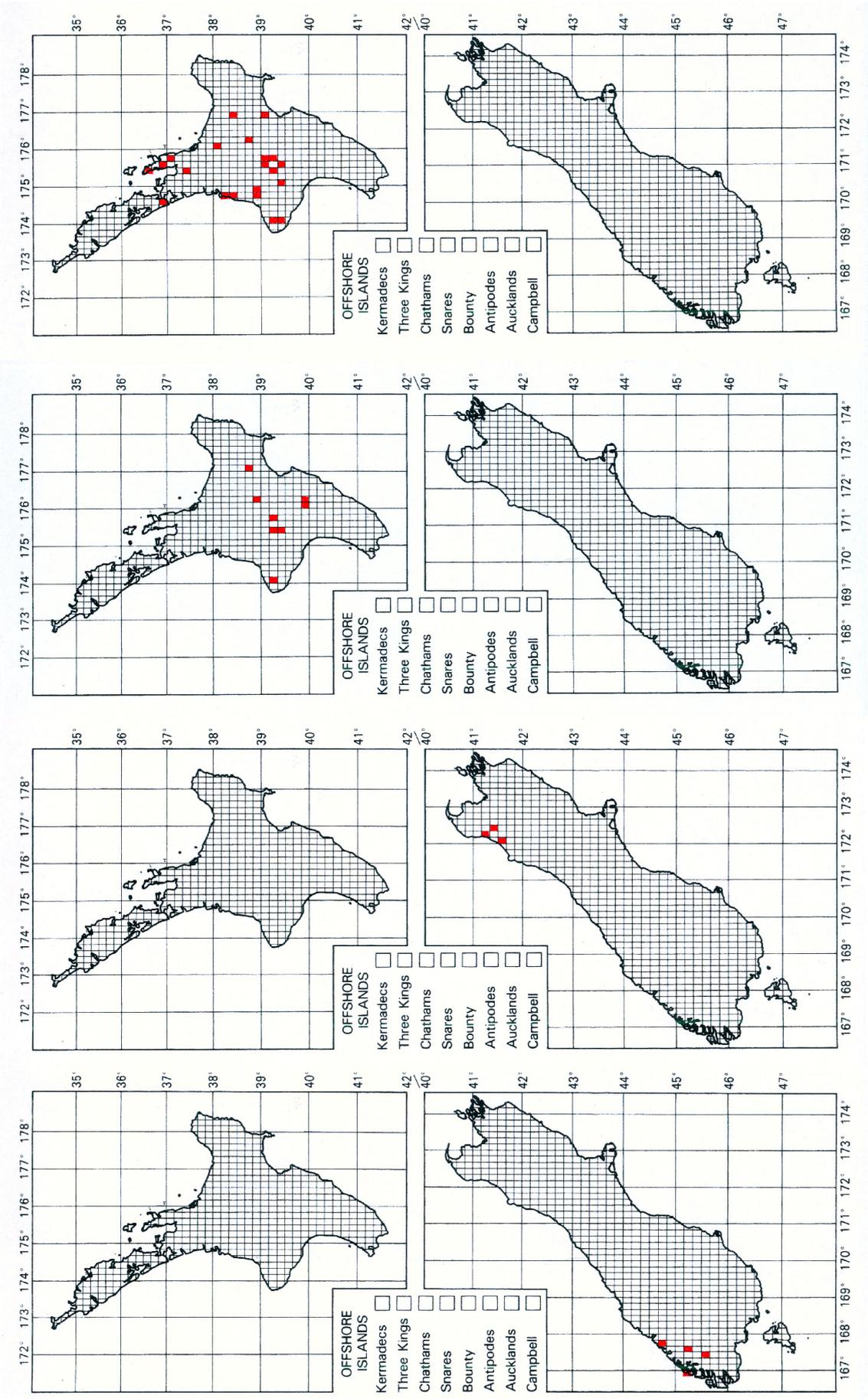
Map 6 *M. falcata*



Map 7 *M. hamadelpha*



Map 8 *M. ngahuru*

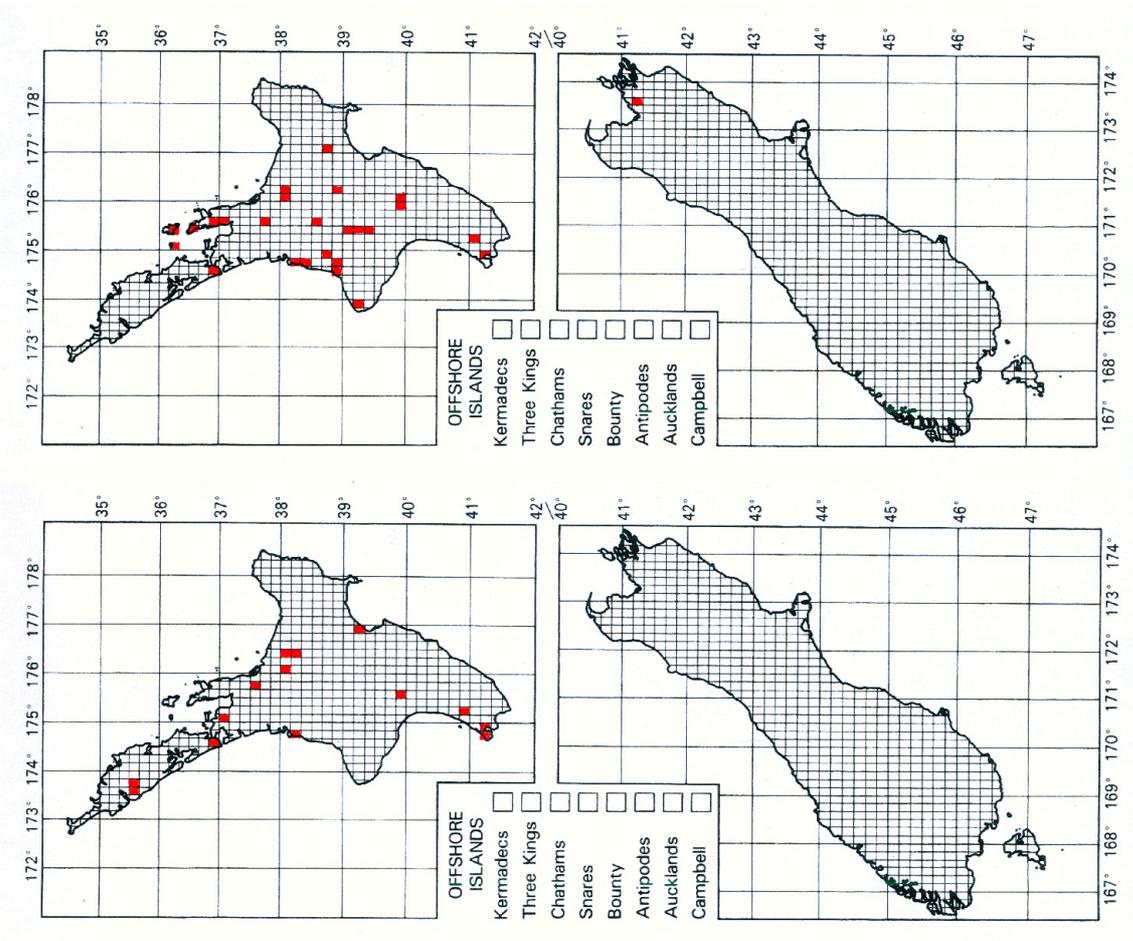


Map 9 *Mnesarchella philpotti*

Map 10 *M. stellae*

Map 11 *M. vulcanica*

Map 12 *M. dugdalei*



Map 14 *M. loxoscia*

Map 13 *M. fusilella*

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Ka āhei te tangata ki te **whakauru tuhituhinga** mehemea kei a ia ngā tohungatanga me ngā rauemi e tutuki pai ai tana mahi. Heoi anō, e wātea ana te Kohinga Angawaho o Aotearoa hei āta tiro tiro mā te tangata mehemea he āwhina kei reira.

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