

Relationships among felt scale insects (Hemiptera:Coccoidea:Eriococcidae) of southern beech, *Nothofagus* (Nothofagaceae), with the first descriptions of Australian species of the *Nothofagus*-feeding genus *Madarococcus* Hoy

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Abstract. Species of southern beech (*Nothofagus*) have been studied extensively because of their importance in understanding southern hemisphere biogeography. *Nothofagus* species support a diverse assemblage of insect herbivores, including more than 30 described species of felt scales (Eriococcidae). We reconstructed the phylogeny of the *Nothofagus*-feeding felt scales with nucleotide sequence data and morphology. All but one of the exclusively *Nothofagus*-feeding species included in the analyses were recovered as a monophyletic group. This clade comprised the genera *Chilechiton* Hodgson & Miller, *Chilecoccus* Miller & González, *Intecticoccus* Kondo, *Madarococcus* Hoy (except for *M. totarae* Hoy), *Sisyrococcus* Hoy and several species of the genus *Eriococcus* Targioni Tozzetti. The genera *Eriococcus* and *Madarococcus* were not recovered as monophyletic. Here we revise *Madarococcus*. We expand the concept of the genus, provide a key to the adult females of the 31 species of *Madarococcus* and, for each named species, provide revised synonymies and any new collection or taxonomic information. We recognise the genus from Australia for the first time and describe the adult females of six new Australian species: *Madarococcus cunninghamii* Hardy & Gullan, sp. nov.; *M. meander* Hardy & Gullan, sp. nov.; *M. megaventris* Hardy & Gullan, sp. nov.; *M. moorei* Hardy & Gullan, sp. nov.; *M. occultus* Hardy & Gullan, sp. nov., and *M. osculus* Hardy & Gullan, sp. nov. We also describe the first-instar nymphs of *M. cunninghamii*, sp. nov., *M. meander*, sp. nov. and *M. moorei*, sp. nov. We transfer 17 species into *Madarococcus* from *Eriococcus*: *M. argentifagi* (Hoy), comb. nov.; *M. cavellii* (Maskell), comb. nov.; *M. chilensis* (Miller & González), comb. nov.; *M. detectus* (Hoy), comb. nov.; *M. eurythrix* (Miller & González), comb. nov.; *M. fagicorticis* (Maskell), comb. nov.; *M. hispidus* (Hoy), comb. nov.; *M. latilobatus* (Hoy), comb. nov.; *M. maskelli*, (Hoy), comb. nov.; *M. montifagi* (Hoy), comb. nov.; *M. navarinoensis* (Miller & González), comb. nov.; *M. nelsonensis* (Hoy), comb. nov.; *M. nothofagi* (Hoy), comb. nov.; *M. podocarpi* (Hoy), comb. nov.; *M. raithbyi* (Maskell), comb. nov.; *M. rotundus* (Hoy), comb. nov. and *M. rubrifagi* (Hoy), comb. nov. We transfer two species from *Sisyrococcus* into *Madarococcus*: *M. intermedius* (Maskell), comb. nov. and *M. papillosus* (Hoy), comb. nov. One species, *M. totarae* (Maskell), is excluded from *Madarococcus*, but cannot at present be placed in another genus and is listed as '*M. totarae* incertae sedis'. We report the first collection of an eriococcid, *M. osculus*, sp. nov., on the deciduous beech, *Nothofagus gunnii*. With respect to biogeography, the results of our phylogenetic analysis are congruent with those obtained from recent analysis of *Nothofagus*; Australian and New Zealand species of *Madarococcus* form a monophyletic group to the exclusion of the South American species, suggesting that long-distance dispersal has played an important role in shaping the distributions of both the *Nothofagus*-feeding felt scales and their hosts.

Introduction

Nothofagus species (southern beeches) are trees, or more rarely shrubs, showing a typical west Gondwanan distribution with species native either to Australia, New Caledonia, New Guinea, New Zealand or South America (Govaerts and Frodin 1998). No extant species are shared between any of these areas. The genus has an excellent fossil record (Hill 2001), including in Antarctica, and its phylogeny and distribution have been studied extensively because of its importance to understanding southern hemisphere biogeography (Humphries 1981; Linder and Crisp 1995; SanMartín and Ronquist 2004; Cook and Crisp 2005; Knapp *et al.* 2005; Heads 2006). It is the only genus in the

Nothofagaceae (previously in Fagaceae) and is sister to the remaining families in the order Fagales (Manos & Steele 1997; Li *et al.* 2004). *Nothofagus* comprises four extant subgenera that are related as follows: (*Lophozonia* (*Fuscospora* (*Nothofagus*, *Brassospora*))) (Manos 1997). Recent molecular modelling suggests that the radiation of the current subgenera and species occurred between 55 and 40 Myr ago (Cook and Crisp 2005). Contrary to the hypothesised sequence and timing for the break-up of western Gondwana, the Australian and New Zealand taxa of both *Lophozonia* and *Fuscospora* are sister taxa, to the exclusion of species from South America. The relaxed molecular

clock estimates for the timing of divergence of Australian and New Zealand taxa is too recent to have been a consequence of vicariance under current models (Cook and Crisp 2005; Knapp *et al.* 2005). Further, the divergence of taxa in New Caledonia from those in South America (*Brassospora* v. *Nothofagus*) appears too recent to be explained by vicariance (Cook and Crisp 2005). Thus, long-distance dispersal appears to have played a role in the current distribution of *Nothofagus*.

Diverse taxa of phytophagous insects are associated with species of *Nothofagus* worldwide (McQuillan 1993). Species of Lepidoptera dominate the mining guild, Lepidoptera and Coleoptera dominate the leaf-chewing guild, whereas species of Coccoidea (scale insects) greatly outnumber all other sap-sucking insects (see appendix in McQuillan 1993). Within Coccoidea, over 60 species in 26 genera distributed among nine families feed on *Nothofagus* (Granara de Willink and Miller 2004; Kondo *et al.* 2006; Ben-Dov *et al.* 2007; Williams 2007). Over half of these species belong to the felt scales or Eriococcidae. Within the Eriococcidae, five genera and 10 species have been described from *Nothofagus* in Chile (Miller and González 1975; Hodgson and Miller 2002; Kondo *et al.* 2006), six of the species present in Chile are known also from Argentina (Miller and González 1975; Gonzalez 2004), and three genera and 24 species are known from *Nothofagus* in New Zealand (Hoy 1962a). No *Nothofagus*-feeding eriococcids have been described from any other countries, although there are specimens from Australia, New Caledonia and New Guinea in museum collections and McQuillan (1993) reported three undescribed species as monophagous on *N. cunninghamii* from Tasmania. McQuillan also reported that no scale insects were known from the deciduous *N. gunnii*, which is restricted to Tasmania. Most of the New Zealand *Nothofagus*-feeding eriococcids are placed in the 'catch-all' genus *Eriococcus* Targioni Tozzetti, but six species are in *Madarococcus* Hoy and two species in *Sisyrococcus* Hoy (Hoy 1962a). Fourteen of the 15 New Zealand *Nothofagus*-feeding *Eriococcus* species, the two species of *Sisyrococcus* and five of the six *Madarococcus* species have been recorded exclusively from *Nothofagus* species. The exceptions are *E. brittini* Hoy, which has been found also on *Coprosma rotundifolia* (first reported here), and *Madarococcus totarae* (Maskell), which has been collected mostly from *Podocarpus totara* and *P. nivalis* (Hoy 1962a). Although *M. totarae* was reported originally on both *Nothofagus* and *Podocarpus* (Maskell 1890), there are no specimens from *Nothofagus* in the New Zealand Arthropod Collection (Hoy 1962a) and it is likely that the record from *Nothofagus* is erroneous. Hoy (1962a) also listed the polyphagous *Eriococcus pallidus* Maskell on *Nothofagus* ? sp. (the slide is labelled 'beech ?') but this is a misidentification of *E. pallidus* and these specimens are probably *E. brittini*. In Chile, four of the five *Nothofagus*-feeding *Eriococcus* species, the two *Nothofagus*-feeding species of *Icelococcus* Miller & González, the monotypic genera *Chilechiton lynnae* Hodgson & Miller and *Intecticoccus viridis* Kondo, and one of the two species of *Chilecoccus* Miller & González have been recorded exclusively from *Nothofagus* species. Here the exceptions are *Eriococcus tholothrix* Miller & González and *Chilecoccus spinosus* Miller & González, both of which have been recorded from *Eucryphia cordifolia* in addition to *Nothofagus*.

Hoy (1962a) first suggested a close relationship between the *Nothofagus*-feeding felt scales of New Zealand and Chile, a notion adopted by subsequent authors (Miller and González 1975; Williams 1985a). In the early cladistic analysis of Humphries *et al.* (1986), the Chilean species *Eriococcus eurythrix* was nested within a clade of New Zealand *Nothofagus*-feeding eriococcids that have spatulate suranal setae. Hodgson and Miller (2002) performed a parsimony analysis of morphological characters of the adult females of several scale insects. They recovered a polyphyletic assemblage of eriococcid species on *Nothofagus* and a sister relationship between the Chilean genus *Chilechiton* and the New Zealand genus *Eriochiton*. The latter result was not supported by the first molecular data (Kondo *et al.* 2006), which placed *Chilechiton* and *Eriochiton* in two separate clades – the Gondwanan and acanthococcid clades of Cook and Gullan (2004).

In this paper we reconstruct the phylogeny of the *Nothofagus*-feeding felt scales using morphology and sequence data from four nuclear loci: elongation factor-1 α (*EF-1 α*); wingless (*wg*); the large ribosomal subunit (28S); and the small ribosomal subunit (18S). We describe the adult females of six new Australian species of *Nothofagus*-feeding eriococcids and the first-instar nymphs of three of these species. Based on the results of the phylogenetic analyses, we place these species in the genus *Madarococcus*, along with four species from Chile (previously in *Eriococcus*) and 24 species from New Zealand (17 species transferred from *Eriococcus*; two species from *Sisyrococcus*; and five species originally described in *Madarococcus*). For each species belonging to the new concept of *Madarococcus*, we provide revised synonymies, any new collection or other data, and diagnostic notes.

Materials and methods

Specimen preparation and examination

Freshly collected specimens were slide-mounted in Canada balsam using the method described in Gullan (1984). Adult females were mounted one specimen per slide; nymphs were mounted several to a slide. Some specimens intended for molecular work were preserved in absolute ethanol and stored below 4°C. After DNA extraction, these specimens were slide-mounted as vouchers.

Specimens used for the morphological and molecular phylogenetic work are listed in Appendix 1. For taxonomic work we mostly used the museum collections of J. W. Beardsley, J. M. Hoy and W. M. Maskell as well as recent collections by P. J. Gullan (PJG), R. C. Henderson (RCH), T. Kondo and N. A. Martin, and we examined type specimens for each of the New Zealand species.

Specimen depositories

- | | |
|------|---|
| ANIC | Australian National Insect Collection, CSIRO, Canberra, Australia |
| BME | Bohart Museum of Entomology, University of California, Davis, USA (also sometimes abbreviated as UCD) |
| BMNH | The Natural History Museum, London, UK |
| BPBM | Bernice P. Bishop Museum, Honolulu, Hawaii, USA |

FRNZ	Forest Research Institute Limited, Rotorua, New Zealand
NZAC	New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand (formerly Department of Scientific and Industrial Research, or DSIR)
MNHM	Museum National d'Histoire Naturelle, Paris
MEUC	Museo Entomológico, Facultad de Ciencias Agronómicas, Universidad de Chile, Santiago, Chile
TASAG	Tasmanian Department of Primary Industries & Water, New Town, Tasmania
USNM	National Museum of Natural History, Smithsonian Institution, housed at the United States Department of Agriculture (USDA), Beltsville, Maryland, USA (now housing VPI collection)
VPI	Virginia Polytechnic Institute and State University, Blacksburg, USA (Coccoidea collection now at USNM)
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia

All material listed in Hoy's (1962a) book, except that recorded for FRNZ, is now in NZAC and all eriococcid slide-mounts in NZAC have been barcoded. The field notebook of J. W. Beardsley is held by PJG.

Taxonomic descriptions and species accounts

Full descriptions with illustrations are provided for six new species from Australia. Responsibility for the recognition and description of these new species rests solely with NBH and PJG who are joint authors of these six new names. Each of the New Zealand and Chilean species have been described and illustrated adequately by Hoy (1962a) and Miller & González (1975). Here we provide revised synonymies, any new information on type specimens, and diagnostic notes for each of the species. Wherever available, we include additional host-plant and locality data available since publication of the original descriptions. For the New Zealand species, most of the new records have been provided by RCH and the data provided for each species are categorized under the New Zealand area codes of Crosby *et al.* (1998) listed from north to south.

The morphological terms for Eriococcidae follow those of Williams (1985b) and Miller and McKenzie (1967). Previous

authors have used the term 'spatulate' to describe the shape of the suranal setae of the *Nothofagus*-feeding eriococcids (Hoy 1962a; Humphries *et al.* 1986; Hodgson and Miller 2002). A spatulate seta is lamellate, with a slender stem gradually broadened to its apex (Torre-Bueno 1989). This term, as it is applied in the present study, encompasses a good deal of variation, especially in terms of the shape of the apex that may be truncate, rounded, acute, or have an irregular, splintered appearance (Fig. 1). On young females of some species the seta may have a very fine flagellate tip that breaks off leaving the tip variously blunt or splintered in appearance. The seta may or may not be broadest at the apex, but will never be broadest at the base. Under certain setal orientations, such as when the edge of the flattened seta is directed towards the observer, spatulate suranal setae may appear evenly attenuated (Fig. 1b).

Measurements were made using an ocular micrometer attached to a compound microscope. All measurements are maximum dimensions (e.g. body width was recorded at the widest point and leg segment lengths were measured along the longest axis) and are expressed as the range. Tarsal length excluded the claw. Spiracle length includes the muscle plate (apodeme). Setal lengths include the setal base. Values given for leg segments are lengths. Illustrations of the adult females and first-instar nymphs of the new Australian species were prepared by NBH with a drawing tube and the Adobe programs Photoshop CS and Illustrator CS. Following the convention for scale insects, each figure displays the dorsal body surface on the left side of the page, and the ventral body surface on the right. An exception was made for *M. megaventrus*, sp. nov. Preliminary sketches of this species following the aforementioned convention proved to be both confusing (legs were on both halves of the page) and unsatisfying (the right half of the page was all but blank). Thus only the dorsal aspect was figured. Enlargements of diagnostic features are located around the margin of each main figure; the sizes of these structures are provided in the text.

Morphological phylogenetic methods

The following species (39 in total) were selected for morphological phylogenetic analysis: 1, exemplars of all known species of Eriococcidae that have spatulate suranal setae and feed exclusively on *Nothofagus* (28 spp. in total; 15 spp. of *Eriococcus*, five

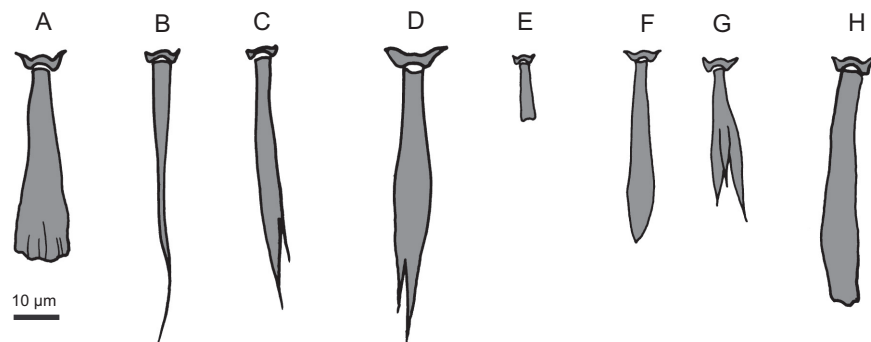


Fig. 1. Spatulate suranal setae of adult *Madarococcus* spp.: A, *M. hispidus*; B, *M. intermedius* with flattened surface perpendicular to observer; C, *M. intermedius* with flattened surface facing observer [figures B, and C, drawn from same specimen]; D, *M. nelsonensis*; E, *M. occultus*; F, *M. osculus* with acute apex; G, *M. osculus* with splintered apex; H, *M. viridulus*.

spp. of *Madarococcus*, two spp. of *Sisyrococcus*; six undescribed spp.); 2, six Chilean species that lack spatulate suranal setae but feed on *Nothofagus* (*Chilechiton lynnae*, *Chilecoccus browni* Miller & González, *Eriococcus chilensis* Miller & González, *E. navarinoensis* Hoy, *E. rhadinothrix* Miller & González and *E. tholothrix* Miller & González); 3, one New Zealand species that lacks suranal setae but feeds on *Nothofagus* (*E. brittini*); 4, the one species of *Madarococcus* that does not feed on *Nothofagus*, or have spatulate suranal setae (*M. totarae*); 5, one species of *Eriococcus* from New Zealand that does not feed on *Nothofagus* (*E. arcanus* Hoy), and 6, as outgroups, two eriococcid species that fell outside of the Gondwanan clade of Cook & Gullan (2004), one of which, *Icelococcus nothofagi* Miller & González, also feeds upon *Nothofagus*. Whenever possible, species were scored from type material, or specimens that had been compared to type material. This was the case for all of the Australian and New Zealand species, although some type speci-

mens of New Zealand species are in very poor condition and thus some microscopic features were scored from more recently collected specimens. Recent collections of the South American species were identified with the literature and, for three of the six Chilean species, with reference to paratypes in the BME and USNM. Details pertaining to the specimens used in the analysis are given in Appendix 1.

Adult females were scored for 32 characters and first-instar nymphs (crawlers) of a subset of taxa (17) were scored for an additional three characters. The character list is available in Table 1, and the data matrix is presented in Table 2 (and a NEXUS file is available as an Accessory Publication on the *Invertebrate Systematics* website). Phylogenies were reconstructed using Bayesian inference methods with MrBayes 3.1.1 (Ronquist & Huelsenbeck 2003), under the mk1 model, with gamma-distributed rates and coding set to variable (Lewis 2001). Each analysis consisted of four Markov chains, three hot

Table 1. Characters used in the morphological phylogenetic analysis

Adult female:

- (1) *Dorsal derm:* (0) membranous; (1) sclerotic
- (2) *Dorsal nodules:* (0) rounded; (1) with acute apices
- (3) *Posterior abdominal segments:* (0) exposed; (1) overlaid by anterior segments
- (4) *Dorsal macrotubular ducts:* (0) present, evenly distributed; (1) present, in crowded transverse rows on anterior abdominal segments; (2) absent
- (5) *Ductule of macrotubular ducts:* (0) with apex flared; (1) with apex acinous (i.e. consisting of minute rounded lobules).
- (6) *Apices of spinose dorsal setae:* (0) acute; (1) blunt; (2) truncate
- (7) *Conical dorsal setae:* (0) present; (1) absent
- (8) *Digitate dorsal setae:* (0) restricted to medial pairs on posterior abdominal segments; (1) scattered over dorsum; (2) absent; (3) arranged in one longitudinal submarginal row on each side of body
- (9) *Slender, slightly curved dorsal setae:* (0) absent; (1) present
- (10) *Number of microtubular ducts at base of each spinose seta:* (0) 0; (1) 1; (2) >1
- (11) *Marginal fringe:* (0) present, fringe remaining tight and linear between eyes; (1) present, fringe staggered between eyes; (2) absent; pairs of enlarged setae arranged transversely on margins of posterior abdominal segments; (3) absent, largest setae present on margin; (4) absent, margin indistinct, marginal setae undifferentiated from dorsal setae
- (12) *Size of dorsum relative to venter:* (0) equal to venter; (1) larger than venter; (2) smaller than venter
- (13) *Frontal lobes:* (0) absent; (1) rudimentary; (2) well developed, digitate; (3) well developed, broad
- (14) *Number setae on apical segment of labium:* (0) >9 pairs; (1) <9 pairs
- (15) *Numerous spinose setae ventrad of margin:* (0) absent; (1) present
- (16) *Ventral abdominal macrotubular duct distribution:* (0) present throughout submargin; (1) found across medial areas of segments; (2) absent; (3) found only posterolateral of vulva; (4) found in submedial regions, either exclusively or in addition to submarginal regions
- (17) *Ventral macrotubular ducts the same size as those on dorsum:* (0) absent; (1) present
- (18) *Ventral macrotubular ducts smaller than those on dorsum:* (0) absent; (1) present
- (19) *Bilocular pores:* (0) absent; (1) present
- (20) *Ventral abdominal pore distribution:* (0) in longitudinal series extending from lobes to coxae, absent from medial areas; (1) present in medial areas
- (21) *Ventral pore sizes:* (0) all of one size; (2) of two sizes
- (22) *Size of translucent pores on hind legs:* (0) small; (1) large
- (23) *Distribution of translucent pores:* (0) restricted to hind coxae; (1) on segments of the hind legs in addition to coxae
- (24) *Suranal setae:* (0) flagellate; (1) spatulate
- (25) *Apex of spatulate suranal setae:* (0) blunt / truncate; (1) acute
- (26) *Cauda:* (0) absent; (1) present
- (27) *Anterior dorsal surface of anal lobes:* (0) simple; (1) with pit
- (28) *Dorsoapical lobe seta:* (0) arising nearer to dorsomedial lobe seta than apical lobe seta; (1) arising nearer to apical lobe seta than dorsomedial lobe seta
- (29) *Number setae on ventral surface of each anal lobe:* (0) 1; (1) 2
- (30) *Anal lobe cuticle:* (0) relatively smooth; (1) rugose
- (31) *Anal plate:* (0) absent; (1) present
- (32) *Body shape:* (0) turbinate; (1) elliptical; (2) round; (3) ovate, with posterior margin forming acute angle with anal lobes

First-instar nymph:

- (33) *Dorsal abdominal setae:* (0) minute; (1) enlarged
- (34) *Dorsal thoracic setae shape:* (0) squat; (1) elongate
- (35) *Ventral lobe seta:* (0) flagellate; (1) spatulate

and one cold (program default), run simultaneously for one million generations, with trees sampled every 1000 generations, discarding the first 100 trees from the burn-in period. The analysis was repeated three times, and recovered similar parameter estimates, suggesting that stationarity had been achieved.

Molecular phylogenetic methods

Exemplars of thirty-two species were represented by sequence data (Appendix 1). Genomic DNA was extracted non-destructively from whole fresh or ethanol-stored, specimens using the 'salting out' method of Sunnucks and Hales (1996) or a DNeasy tissue kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions, except that the cuticle of each specimen was removed from the extraction mix after the digestion step. Vouchers of specimens will be deposited in the ANIC. Four

nuclear gene regions (partial elongation factor-1 α (*EF-1 α*), partial wingless (*wg*), partial small subunit ribosomal rRNA (SSU rRNA, 18S) and partial large subunit ribosomal rRNA (LSU rRNA, 28S) were amplified and sequenced using the primer pairs listed in Table 3. In addition, part of the mitochondrial small rRNA gene (12S) was amplified using primers 12Sf and 12Sr (Table 3) but was not included in analyses because of the very high level of divergence and length variation among taxa that, in addition to a very high AT bias, made alignment ambiguous. Sequencing was performed on an ABI 377 or 3100 automated DNA sequencer using BigDye chemistry, as per the manufacturer's instructions. All four gene regions could not be successfully amplified or sequenced for all relevant taxa, despite altering PCR conditions and trying different primer combinations. This is not unusual for scale insects. In addition,

Table 2. Morphological matrix

Taxon	Characters			
	0000000001 1234567890	11111111112 1234567890	2222222223 1234567890	33333 12345
<i>Chilecoccus browni</i>	0?00010210	4100141100	0110?00000	12???
<i>Chilechiton lynnae</i>	0?02010210	0100020100	0110?00100	12???
<i>Eriococcus arcanus</i>	0100100200	1100041101	0100?01000	01???
<i>E. argentifagi</i>	0000020202	2010001001	0011001100	0002?
<i>E. brittini</i>	0000110201	4100011101	0100?00001	01???
<i>E. cavellii</i>	0000010202	3020101000	0011000100	02111
<i>E. chilensis</i>	0000011210	1100041101	1010?00000	01???
<i>E. coccineus</i>	0000120100	1121011111	0000?10010	01???
<i>E. detectus</i>	0002010101	0120001001	0011001101	02???
<i>E. eucalypti</i>	0000?12202	4000040101	0010?00000	01???
<i>E. fagicorticis</i>	0100010202	1010001001	0011100101	01101
<i>E. hispidus</i>	0000020202	3020101001	0011000100	02111
<i>E. latilobatus</i>	000001?100	1110001000	0011001100	0201?
<i>E. maskelli</i>	0100020002	2020001001	0011000100	01???
<i>E. montifagi</i>	0002011100	01?0001001	0011001101	02???
<i>E. navarinoensis</i>	0000011210	1100041101	1010?00?00	01???
<i>E. nelsonensis</i>	0000020002	2020001001	0011100100	00101
<i>E. nothofagi</i>	0000020002	2010001001	0011000101	00011
<i>E. podocarpi</i>	0100020202	3020001001	0011000100	01???
<i>E. raithbyi</i>	00000?1200	10?0001001	0011001101	01110
<i>E. rhadinothrix</i>	0000011210	1100041101	1010?00000	01???
<i>E. rotundus</i>	0000021102	1110001000	0011001100	02011
<i>E. rubrifagi</i>	0000020102	2020001001	0011000100	00???
<i>E. tholothrix</i>	0000112200	4000040101	0010?00000	01???
<i>Intecticoccus nothofagi</i>	0002?10200	1121020011	0110?10011	00???
<i>Madarococcus cruriamplus</i>	0002?11102	0010020001	0011101100	01???
<i>M. cunicularius</i>	1002?01200	1200020000	0011000100	01???
<i>M. cunninghamii</i>	0002010202	3010031000	0011101101	03010
<i>M. eurythrix</i>	0000011210	1110011000	0011000100	01010
<i>M. maculatus</i>	0002?10002	0010020000	0011101100	01???
<i>M. meander</i>	1000011200	1200020000	0011?00100	01011
<i>M. megaventris</i>	1000001200	1200020001	0010?00100	01???
<i>M. moorei</i>	0002010101	0110001001	0011000100	02010
<i>M. occultus</i>	0000011210	1100011001	0011000000	01???
<i>M. osculus</i>	0000001202	0020001000	0011100100	01???
<i>M. pulchellus</i>	0002?10201	3020020001	0011001101	01???
<i>M. totarae</i>	0002?10300	0130040101	0100?00000	0?000
<i>M. viridulus</i>	0002?10201	3020020001	0011001101	0111?
<i>Sisyrococcus intermedius</i>	00110?0102	1110020001	0011000100	00010
<i>S. papillosus</i>	00110?0202	4110?20001	0011000100	00???

wg was recovered only as multiple copies in several taxa, and these were excluded from analyses.

Sequences were edited in Sequencher v4.5 (Gibbs and Cockerill 1995) and aligned by eye using Se-Al (Rambaut 1998). Bayesian, maximum likelihood (ML) and maximum parsimony (MP) methods of phylogeny estimation all assume that base frequencies do not differ among taxa (stationarity). We therefore tested for non-stationarity using the chi-square test as implemented in PAUP* (Swofford 2003). *Madarococcus pulchellus* and *M. viridulus* were identical for all sequences obtained; therefore they were treated as a single composite taxon in the analyses.

Phylogenies were estimated for each dataset separately using MrBayes v3.1 (Ronquist and Huelsenbeck 2003). We used a GTR+I+G model for each partition (defined below) and ran two simultaneous analyses of eight chains for ten million generations, sampling trees every 1000th generation. Runs were checked for convergence graphically and by comparing Harmonic means. Trees saved during the estimated burn-in period (between four and seven million generations) were discarded before further analyses.

The expansion regions of SSU and LSU rDNA of scale insects show extensive length variation, making alignment and assessment of homology among coccoids difficult. In addition, positional homology does not always equate with structural homology in scale insects (Cook unpublished data). Analyses were therefore run without the ambiguously aligned regions. We developed a secondary structure model of 28S for eriococcids (Cook unpublished data) and used this to partition the data by stems, terminal loops and internal bulges. We ran analyses with and without defining these partitions. The intron-exon boundaries of *EF-1 α* were identified and the introns were excluded from further analyses because they varied in length and base composition among taxa and could not be unambiguously aligned. There were no introns present in the region of wingless amplified (390 bp). We partitioned the exon data of both *EF-1 α* and *wg* by codon position for analysis in MrBayes. First and second positions were combined because each comprised only a few variable positions – there was a lack of power

to estimate separate models – and the two positions did not differ in base composition. Third positions were assigned an independent partition. Each partition was allowed a different, unlinked GTR+I+G model in Bayesian analyses. We also conducted an ML analysis of the *EF-1 α* data using a GTR+I+G model with parameters estimated using Modeltest (Posada and Crandall 1998). We used 24 trees derived using MP as the starting trees for the ML heuristic search and had no further constraints.

Individual gene trees were compared to determine if there was any supported conflict between gene partitions. Gene regions were determined to be compatible and Bayesian analyses of concatenated sequence data were conducted as follows. The ‘three-gene’ dataset comprised 18S, 28S and *EF-1 α* and included only those taxa for which we had sequences for all three genes. Similarly, the ‘four-gene’ dataset comprised only those taxa for which we had all four gene regions (18S, 28S, *EF-1 α* , *wg*). A 1707 base-pair ‘supermatrix’ of all four gene regions (353bp *wg*, 375bp *EF-1 α* , 608 bp 18S, 371bp 28S) comprised all taxa for which two or more gene regions had been sequenced. In each concatenated-data matrix, 18S and 28S were each allowed their own GTR+I+G model because they had different base frequencies. Two codon-position partitions (1st + 2nd positions; 3rd position) were used for the two protein-encoding gene regions.

Combined morphological and molecular phylogenetic methods

We took two approaches to combining our morphological and DNA sequence data. First we used a ‘DNA filter’, in which morphological data were added only to taxa represented by sequence data in the four-gene supermatrix. We then estimated the phylogeny with a MrBayes search in which each of the previously stated DNA partitions and the morphological partition was allowed its own model. In our second approach, we used a ‘DNA scaffold’ to place taxa represented only by morphological data while preserving the underlying structure of the tree inferred from the sequence data (e.g. Springer *et al.* 2001; Manos *et al.* 2007). Each node recovered with $\geq 95\%$ PP from

Table 3. Primers used in this study
The forward primer is listed first for each pair

Primer	Sequence	Reference
<i>wg</i>		
scale_wg_F	CTGGTTCGTGCACGACGMGRACSTGYTGATG	This study
modLEPWG2	ACTICGCARACCARTGGAATGTRCA	Brower, modified by Campbell (Brower & DeSalle 1998)
<i>EF1α</i>		
scutA_F	ATTGTGCTGCTGGTACCGGTGAATT	This study
rcM52.6	GCYTCGTGGTGCAATYTCSAC	Cho <i>et al.</i> (1995)
28S		
Bel28S-D2for	AGAGAGAGTTCAAGAGTACGTG	Belshaw & Quicke (1997)
28S-D2rev	TTGGTCCGTGTTTCAAGACGGG	Belshaw & Quicke (1997)
18S		
2880	CTGGTTGATCCTGCCAGTAG	Tautz <i>et al.</i> (1988)
Br	CCGCGGCTGCTGGCACCAGA	von Dohlen & Moran (1995)
12S		
12SF	AACTAGGATTAGATACCCTA	This study
12SR	GACGGGCGATRTGTACA	This study

the analysis of the four-gene supermatrix was enforced as a backbone constraint in a Maximum Parsimony (MP) search implemented in PAUP*. If a species was represented by multiple exemplars in the DNA dataset, only one was included in the DNA scaffold analysis. *Madarococcus pulchellus* and *M. viridulus* also were treated as a single entity here because they were treated as a single composite taxon in the DNA analyses, and did not differ in any features used in the morphological analysis. We performed a heuristic search consisting of 100 random addition sequences followed by TBR branch swapping, with no limit placed on the number of saved trees. Support for all relationships was estimated with 100 non-parametric bootstrap replicates. Each bootstrap search was the same as that used to infer the MP tree, but with only 20 random addition sequences and no topological constraints.

Results

Morphological phylogeny

The Bayesian analysis returned a majority-rule consensus tree (Fig. 2A) having very little resolution amongst the Australian and New Zealand species, and few strongly supported relationships in general. All of the exclusively *Nothofagus*-feeding species except *Icelococcus nothofagi* were recovered as monophyletic, although with low support (PP = 0.78). *Madarococcus sensu* Hoy (1962a) was not monophyletic; *M. cunicularius* was sister to two new gall-inducing Australian species (*M. meander*,

sp. nov.; *M. megaventris*, sp. nov.) (PP = 0.99) and *M. totarae* was more distantly related to *Madarococcus* than several of the included Chilean species. A new Tasmanian species (*M. occultus*, sp. nov.) was reconstructed as sister to the Chilean *E. eurythrix* + the rest of the Australian and New Zealand *Nothofagus*-feeding species with spatulate suranal setae. Other strongly supported relationships were: 1, the Gondwanan clade (PP = 1.0); 2, the *Nothofagus*-feeding species with spatulate suranal setae (PP = 1.0); 3, *Sisyrococcus intermedius* + *S. papillosus* (PP = 1.0), and 4, *Chilechiton lynnae* + *Chilecoccus browni* (PP = 0.99).

Molecular phylogeny

Of the alignment of 1707 bp, there were 659 variable positions of which 479 were parsimony informative (Table 4). Each gene region contributed more than 100 variable characters. There was not significant non-stationarity within any of the gene regions (Table 4). However, base frequencies differed among gene partitions, and a comparison of corrected (HKY85) v. uncorrected ('p') distances suggested some saturation. Therefore, Bayesian analysis was preferred over parsimony. Bayesian phylogenetic analysis of the four-gene supermatrix returned a well resolved phylogeny, with strong support for nodes of interest (Fig. 3). *Icelococcus nothofagi* did not cluster with the other *Nothofagus*-feeding eriococcids and was the well supported sister taxon of the New Zealand genus *Eriochiton* (PP = 1.0). All other eriococcid taxa that feed exclusively on *Nothofagus* were recov-

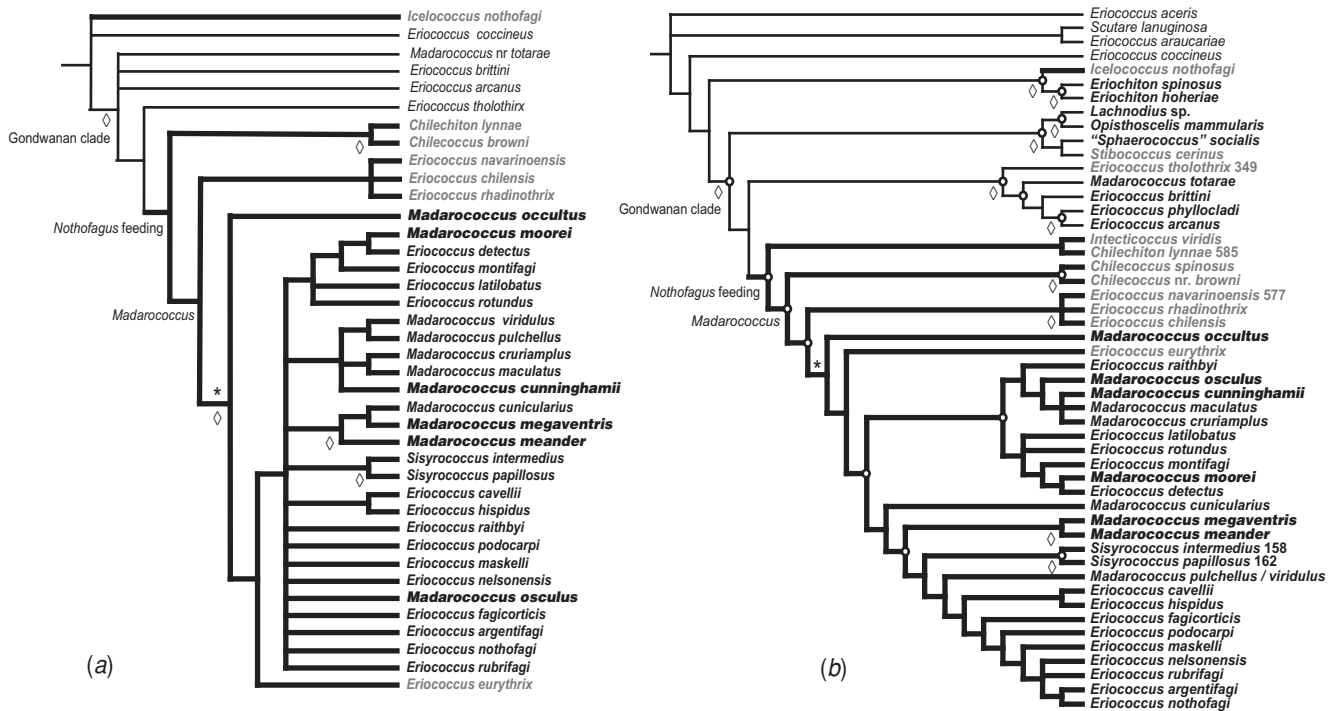


Fig. 2. A, Majority-rule consensus tree returned from Bayesian analysis of morphological data. Posterior probabilities ≥ 0.95 represented by diamond below node. B, Strict consensus of MP trees recovered from DNA scaffold analysis. Open circles correspond to backbone constraint. Bootstrap proportions ≥ 0.70 represented by diamond below node. *Nothofagus*-feeding taxa subtended by bold branches. Names of South American taxa in grey; names of Australian taxa black, in heavy bold; names of New Zealand taxa in black. Taxon names used on these two trees comprise those in the literature before this study as well as those of new species described herein; our broadened concept of *Madarococcus* is indicated by the node labelled with this genus name. An asterisk indicates the clade in which adult females have spatulate sural setae.

Table 4. The alignment length, *X*-squared value (testing for non-stationarity), number of variable characters and number of parsimony-informative characters for each locus

Gene region	Length of alignment	<i>X</i> -square	Variable	Parsimony informative
<i>wg</i>	353	0.74	157	119
<i>EF-1α</i> exons	375	1	146	129
18S	608	1	129	87
28S	371	1	227	144

ered as a monophyletic group (PP = 1.0), falling within the Gondwanan clade previously recognised by Cook and Gullan (2004). Of these, Australian and New Zealand taxa formed a monophyletic group to the exclusion of the South American taxa (PP = 1.0), but Australian and NZ taxa did not form reciprocally monophyletic groups because *M. cunicularius* is separated from the rest of the New Zealand taxa. The Australia–NZ cluster comprised species currently assigned to *Eriococcus*, *Madarococcus*, *Sisyrococcus* and the Australian taxa described in this paper. *Madarococcus sensu* Hoy was not monophyletic. *Madarococcus totarae* (podocarp-feeding, New Zealand) did not fall with other members of the genus as it is currently circumscribed, but was part of a clade from New Zealand that includes other species that also feed on podocarps (*E. arcanus* and *E. phyllocladi*) (PP = 1.0). *Sisyrococcus* and some species currently assigned to *Eriococcus* fell within the clade of *Nothofagus*-feeding *Madarococcus*.

The above relationships were all recovered from the four-gene analysis and three-gene analysis, and none were contradicted by supported conflict in individual gene trees.

Combined morphological and molecular phylogeny

The DNA filter phylogeny inferred from the Bayesian analysis of the four-gene + morphology supermatrix (not shown) was nearly identical to that inferred from the sequence data alone. Only one relationship strongly supported by the sequence data was not also strongly supported by the sequence + morphological data: the two species of *Chilecoccus* sister to *E. eurythrix*, *E. navarinoensis*, and the Australia–NZ *Nothofagus*-feeding species (PP = 0.88). No relationship not supported by the sequence data alone was supported with the addition of the morphological data.

The DNA scaffold MP analysis returned 416 trees, each of length 1487. The strict consensus (Fig. 2B) was well resolved, but, as was the case for the morphological analysis, support was generally low. The monophyly of the Chilean species *E. chilensis*, *E. navarinoensis*, and *E. rhadinotrix* was well supported (BS = 0.75). In contrast to the molecular phylogeny, in which weak support was recovered for a sister relationship between the Chilean species *E. eurythrix* and *E. navarinoensis*, here *E. eurythrix* was found to be more closely related to the Australia–NZ *Nothofagus*-feeding species, although without bootstrap support. The new Tasmanian species, *M. occultus*, sp. nov., was recovered as sister to *E. eurythrix* + the Australia–NZ *Nothofagus*-feeding species (BS = 0.52). The lack of reciprocal monophyly between the Australia and New Zealand species is more pronounced here than in the molecular phylogeny.

Discussion

We have found both morphological and molecular evidence for the monophyly of a group of more than 30 species of felt scales that feed exclusively on *Nothofagus*. The phylogeny inferred from morphology is largely unresolved and unsupported, but the congruence of phylogeny estimates based upon independent sources of data, along with the coincidence of *Nothofagus* feeding, increase our confidence in the hypothesis. This phylogenetic study further resolves the taxonomic problems surrounding Eriococcidae, and *Eriococcus* in particular. Several species with the generic name *Eriococcus* are recovered within the Gondwanan clade (Fig. 3), but we know from previous studies (Cook and Gullan 2004) that the type species of *Eriococcus*, *E. buxi* (Boyer de Fonscolombe), falls outside the Gondwanan clade and is therefore not part of the cluster. Analysis of both the morphological and sequence data reconstructed *Chilechiton* and *Chilecoccus* as sister to a clade comprised of several *Eriococcus* and *Madarococcus* species in addition to the two species of *Sisyrococcus*. Here we advance a broadened concept of *Madarococcus* for this clade. *Madarococcus totarae* did not cluster with the other species of *Madarococcus*, but rather clustered with another group of species currently ascribed to *Eriococcus*: the Chilean species *E. tholothrix*, and the New Zealand species *E. arcanus*, *E. brittini*, and *E. phyllocladi*. As mentioned above, *E. brittini* has been collected on *Nothofagus solandri* and *Coprosma rotundifolia*. The two other New Zealand species (*E. arcanus* and *E. phyllocladi*) feed exclusively on plants in the Podocarpaceae, as does *M. totarae*. Three described New Zealand species, which have not been included in this study, also feed exclusively on podocarps: *E. dacrydii* Hoy, *E. matai* Hoy, and *E. parvulus* Hoy (Hoy 1962a). Until the taxonomy of this group is revisited, we have chosen to leave *M. totarae* as *incertae sedis*.

More than half of the species we have included in our new concept of *Madarococcus* are represented in this study by only morphological data. Morphology alone was not sufficient to infer a well resolved phylogeny with confidence, and so we sought to combine our morphological and DNA sequence data. Simulation studies (Huelsenbeck 1991; Wiens 2003) have shown that analyses that include taxa with highly incomplete data with fewer than 100 characters frequently recover trees with low accuracy and resolution. In this study, we had only 35 morphological characters. Not surprisingly, our initial attempts to infer the phylogeny of *Madarococcus* and its relatives from a highly incomplete data matrix returned estimates with little resolution and support. Therefore, we decided to use two other methods. In our DNA filter approach, we added morphological data only for those taxa represented by sequence data. The phylogeny inferred by the DNA filter method is valuable in the sense that all available data for the included taxa were taken into consideration, but this approach does not allow us to recover relationships amongst taxa represented by only morphology. For that purpose, we used the DNA scaffold method. Our MP DNA scaffold search returned a phylogeny estimate with 25 / 29 nodes resolved within *Madarococcus* (only four of which were constraint nodes), a substantial improvement over the phylogeny inferred from only morphology, which recovered 15 / 30 possible nodes. Nevertheless,

a synapomorphy for this group. Second, *Madarococcus* and its South American relatives show a similar biogeographic pattern to their host taxa. In both *Nothofagus* and the scale insects, Australian and New Zealand taxa are more closely related to each other than either is to South America taxa. This pattern is incongruent with the vicariance hypothesis that Australia and South America were joined more recently, via Antarctica, than their connections with New Zealand. Thus, it appears likely that dispersal across the Tasman Sea might have played a role in the current distribution of *Madarococcus* in both Australia and New Zealand.

In their morphological phylogenetic analysis, Hodgson and Miller (2002) recovered the Chilean species *Chilecoccus lynnae* as sister to the New Zealand tribe Eriochitonini, comprised of the genera *Eriochiton* and *Neoerichiton* Hodgson, and they suggest expanding the tribe to include *Chilechiton*. Our results are congruent with those of Kondo *et al.* (2006), which do not support a close relationship between *Chilechiton* and *Eriochiton*.

In deciding which species to include in *Madarococcus*, we sought to 1, name a monophyletic group, and 2, disturb the existing generic classification as little as possible. We also recognise the importance of a generic concept that is easy to define morphologically. In this case, reconciling the clades reconstructed by phylogeny with diagnostic morphology was not simple and so our concept is complex.

Taxonomy

Genus *Madarococcus* Hoy

Madarococcus Hoy, 1962a: 15, 21, 151–163, 200.

Type species: *Rhizococcus pulchellus* Maskell, by original designation.

Diagnosis

The adult females of 27 of the 31 species of *Madarococcus* can be distinguished by the spatulate shape of the suranal setae, although these can be difficult to distinguish in *M. intermedius*, comb. nov. and *M. papillosus*, comb. nov. The species that do not have spatulate suranal setae are *M. chilensis*, comb. nov., *M. megaventrtris*, sp. nov., *M. navarinoensis*, comb. nov. and *M. rhadinothrix*, comb. nov. The adult females of *M. megaventrtris*, sp. nov. are found within distinctive finger-shaped galls on the leaves of *N. moorei* in Australia. The ventral body surface is greatly expanded and projects forward up to several times the length of the dorsum to fill the gall cavity. The remaining three species lacking spatulate suranal setae are Chilean, and can be recognised by having two sizes of quinquelocular pores on the venter and tubular ducts on the ventral surface of the abdomen that are smaller than those on the dorsum. In all *Madarococcus* species (except *M. occultus*, sp. nov., *M. chilensis*, *M. navarinoensis*, and *M. rhadinothrix*) the dorsoapical (distal medial) anal lobe seta arises closer to the caudal seta than to the dorsomedial (proximal medial) anal lobe seta, although this feature is not exclusive to *Madarococcus* and is shared by several *Eriococcus* species, e.g. *E. araucariae* Maskell, *E. celmisiae* (Maskell), *E. montanus* Hoy and *E. pimeliae* Hoy. In addition, the adult females of 20 of the 31 *Madarococcus* species have 1–5 microtubular ducts associated with the bases of at least some enlarged

dorsal setae, although this characteristic is not unique to *Madarococcus*. The association of enlarged dorsal and/or marginal setae with microtubular ducts occurs in several other eriococcid taxa in Australia (e.g. *E. eucalypti* Maskell group), Chile (*Stibococcus cerinus* Miller & González; *Orafortis* Hardy) and New Zealand (e.g. *E. brittini* Hoy, *E. chathamensis* Hoy, *E. crenilobatus* Hoy, *E. matai* Hoy, *E. multispinosus* (Maskell), *E. pallidus* Maskell, and *E. phyllocladi* Maskell). An ecological characteristic uniting the species of *Madarococcus* is that they feed exclusively on *Nothofagus* species, however in South America several other eriococcids occur on *Nothofagus*, including *Chilechiton lynnae*, both *Icelococcus* species, both *Chilecoccus* species, *Eriococcus tholothrix* and *Intecticoccus viridis* (Miller and González 1975; Hodgson and Miller 2002; Kondo *et al.* 2006).

Description

Body shape variable: rotund, turbinate, ovate, elliptical, some species with dorsal surface of anterior abdominal segments folded over posterior abdominal segments. Eyespot on or near margin. Antennae 6- or 7-segmented. Frontal lobes (interantennal lobes) papilliform, arising adjacent to medial margin of scape; absent in some species. Labium either 3-segmented or composed of two fused segments. Legs well developed; distribution of translucent pores variable, in most species found on hind coxae, femora and proximal portions of tibiae. Vulva between abdominal segments VII and VIII. Anal ring bearing six or eight setae. Suranal setae spatulate (for definition of spatulate see Materials and Methods) on all species except *M. chilensis*, *M. megaventrtris*, sp. nov., *M. navarinoensis* and *M. rhadinothrix*. Anal lobes variable, several species have a conspicuous pit in dorsal surface near anterior margin; all lobes with three dorsal setae (dorsomedial, dorsolateral and dorsoapical), one apical seta (or caudal seta) and one ventral seta; dorsoapical seta arising closer to apical seta than dorsomedial seta except in *M. occultus*, sp. nov., *M. chilensis*, *M. navarinoensis*, and *M. rhadinothrix*.

Dorsal derm sclerotic or membranous and usually nodulose, nodules either rounded or conical. Dorsal setae ranging from minute and digitate to enlarged and spinose; apices acute, blunt or truncate. Marginal setal fringe present or absent. Quinquelocular pores absent from dorsum (except *M. intermedius*). Macrotubular ducts present or absent, if present with variably sclerotic cup-shaped vestibule and flared inner ductile. Microtubular ducts always present, 1–5 opening at bases of enlarged dorsal setae in most, but not all, species.

Ventral derm membranous. Ventral setae flagellate or spinose; in transverse rows across each abdominal segment, enlarged medial pair on each segment present or absent, scattered along margin, group of setae medial of each coxa, longitudinal band of elongate setae on medial portion of head. Venter with multilocular pores quinquelocular or trilocular; occurring on abdomen either as a submedial, longitudinal series running from anal lobes to hind coxae on each side of body, or more evenly present medially. Quinquelocular pores of one or two size-classes. Ventral macrotubular ducts present or absent. Macrotubular ducts on ventromedial surface of abdomen present or absent, if present may be distinct from those on lateral portions of venter and dorsum. Microtubular ducts along margin, or absent.

Habit

Adult females either forming test (= sac), naked, or inducing gall (Fig. 4); found on leaf surfaces, stems, leaf axils or bark crevices. Some species with glassy filaments born on enlarged dorsal and marginal setae. Body colour varies from pale green to yellow to brown, sometimes changing with age; some species with striking white patterns on dorsum. Occurring exclusively on *Nothofagus*.

Key to species of *Madarococcus* based on adult females

(drawing from the keys of Hoy (1962a) and Miller and González (1975))

1. Venter with two sizes of quinquelocular pores; suranal seta not spatulate; macrotubular ducts present on dorsum and venter, ducts on ventral surface of abdomen smaller than those on dorsum 2
 - Venter with only one size of quinquelocular pores; suranal setae usually spatulate (Fig. 1); if macrotubular ducts present on dorsum and venter, ducts on ventral surface of abdomen same size as those on dorsum 4
2. Dorsomedial setae on abdomen each *c.* equal in length to the largest marginal setae
 - *M. chilensis* (Miller & González), comb. nov.
 - Dorsomedial setae on abdomen each noticeably shorter than largest marginal setae 3
3. Antennae 6-segmented; abdominal segment V with 9–14 enlarged setae; ratio of hind tibia to hind tarsus 0.7–0.8; enlarged setae on dorsomedial areas of head and thorax each *c.* same size as those along margin of abdomen
 - *M. rhadinothrix* (Miller & González), comb. nov.
 - Antennae 7-segmented; abdominal segment V with 19–31 enlarged setae; ratio of hind tibia to hind tarsus 0.9–1.1 enlarged setae on dorsomedial areas of head and thorax each noticeably smaller and more slender than those along margin of abdomen
 - *M. navarinoensis* (Hoy), comb. nov.
4. Ventral macrotubular ducts arranged in transverse rows across abdominal segments; enlarged dorsal setae curving slightly; from South America or Australia . . 5
 - Ventral macrotubular ducts (if present) never found in medial portions of abdominal segments; enlarged dorsal setae straight or absent; from Australia or New Zealand 6
5. Anal ring with eight setae; translucent pores on hind legs *c.* 1 µm in diameter; from South America.
 - *M. eurythrix* (Miller & González), comb. nov.
 - Anal ring with six setae; translucent pores on hind legs *c.* 5 µm in diameter; from Australia
 - *M. occultus* Hardy & Gullan, sp. nov. (Fig. 12)
6. In life, dorsal surface of anterior abdominal segments folded back over posterior abdominal segments, anal lobes concealed from above; dorsal macrotubular ducts arranged into tight transverse lines on anterior abdominal segments 7
 - Abdomen and dorsal macrotubular ducts not as above. . 8
7. Enlarged setae forming marginal fringe, most distinct on posterior abdominal segments, setae becoming more irregularly positioned cephalad, only a few similar setae found on dorsum; narrow band of quinquelocular pores on dorsomedial surface of head
 - *M. intermedius* (Maskell), comb. nov.
 - No distinct marginal fringe present, *c.* 500 enlarged setae covering dorsum; quinquelocular pores absent from dorsal surface of head
 - *M. papillosus* (Hoy), comb. nov.
8. Dorsal derm sclerotic; venter larger than dorsum in mature specimens; all dorsal setae inconspicuous, submedial setae lacking from majority of abdominal segments; inducing galls. 9
 - Dorsal derm membranous; size of venter less than or equal to that of dorsum in mature specimens; submedial setae present on majority of abdominal segments; inducing galls or not 11
9. Suranal setae flagellate; venter extending anterad for distance much greater than that between eyes and anal lobes; macrotubular and microtubular ducts scattered over dorsum.
 - *M. megaventris* Hardy & Gullan, sp. nov. (Fig. 9)
 - Suranal setae spatulate; venter larger than dorsum, but not directed anteriorly for a distance greater than that between eyes and anal lobes; macrotubular or microtubular ducts confined to margin 10
10. Macrotubular ducts present on dorsum just mesad of margin; only one marginal seta present on each side of each abdominal segment; anal lobes with truncate apices and inner margin straight, parallel to longitudinal body-axis.
 - *M. meander* Hardy & Gullan, sp. nov. (Fig. 7)
 - Microtubular ducts present on dorsum just mesad of margin; multiple marginal setae present on each side of each abdominal segment; anal lobes conical
 - *M. cunicularius* Hoy
11. Dorsal macrotubular ducts absent, in life not forming a test 12
 - Dorsal macrotubular ducts present, in life forming a test or partial test 19
12. Ventral macrotubular ducts either absent or limited to a pair on either side of abdomen posterolateral of vulva 13
 - Ventral macrotubular ducts found throughout submarginal zones 17
13. Ventral macrotubular ducts present posterolateral of vulva; caudal seta shorter than dorsoapical lobe seta; posterior body margin near anal lobes curving slightly cephalad
 - *M. cunninghamii* Hardy & Gullan, sp. nov. (Fig. 5)
 - Ventral macrotubular ducts completely absent; caudal seta longer than dorsoapical lobe seta; body shape elliptical 14
14. Most or all enlarged dorsal setae on margin; anal lobes as broad at base as long; dorsal pit near anterior margin of each anal lobe absent or inconspicuous 15

- Dorsum densely beset with enlarged setae; anal lobes longer than basal width; dorsal pit near anterior margin of each anal lobe well developed 16
15. Enlarged setae confined to margins; minute setae scattered over dorsum *M. cruriamplus* Hoy
Enlarged setae present on dorsum, in one medial and one submedial row on each side of body; minute dorsal setae confined to posterior abdominal segments
. *M. maculatus* (Maskell)
16. Dorsal setae of two distinct size classes
. *M. viridulus* Hoy
Dorsal setae may vary slightly in size, but not in two discrete classes *M. pulchellus* (Maskell)
17. Enlarged setae completely absent from dorsum
. *M. montifagi* (Hoy), comb. nov.
Enlarged setae present on dorsum 18
18. Dorsal surface of each anal lobe with conspicuous pit near anterior margin; translucent pores present on proximal portions of hind tibiae
. *M. detectus* (Hoy), comb. nov.
Dorsal surface of each anal lobe simple, without conspicuous pit near anterior margin; translucent pores absent from hind tibiae
. *M. moorei* Hardy & Gullan, sp. nov. (Fig. 10)
19. Flagellate setae present on dorsal surface of head and thorax; anal lobe cuticle extremely rugose, lateral lobe seta minute *M. raithbyi* (Maskell), comb. nov.
Flagellate setae never present on dorsum; anal lobe cuticle and lateral lobe seta variable, but generally not as above 20
20. Labium composed of two fused segments, basal segment absent; length of antennal segment III > combined length of segments I + II; Australia
. *M. osculus* Hardy & Gullan, sp. nov. (Fig. 13)
Labium 3-segmented, basal segment indicated by basal segment setae; length of antennal segment III < combined length of segments I + II; New Zealand 21
21. Marginal fringe present, represented by several setae on each abdominal segment 22
Marginal fringe absent, although one enlarged marginal seta may be present on each side of each abdominal segment 24
22. Enlarged dorsal setae present on abdomen in addition to head and thorax; marginal fringe disintegrating cephalad; dorsal derm with conical nodules
. *M. fagicorticis* (Maskell), comb. nov.
Enlarged dorsal setae, if present, restricted to head and thorax; marginal fringe complete, becoming only slightly staggered along anterior margin of head; dorsal derm nodules rounded 23
23. Enlarged dorsal setae no more than four in number
. *M. rotundus* (Hoy), comb. nov.
Enlarged dorsal setae greater than 10 in number
. *M. latilobatus* (Hoy), comb. nov.
24. Numerous spinose setae present ventrad of margin 25
Spinose setae confined to dorsum and margin 26
25. Majority of disc pores trilocular; ventral abdominal setae flagellate, longest setae 35–50 µm long; width of hind coxae less than 1.5× width of mid coxae
. *M. hispidus* (Hoy), comb. nov.
Majority of disc pores quinquelocular; ventral abdominal setae robust, longest setae 15–25 µm long; width of hind coxae greater than 1.5× width mid coxae
. *M. cavellii* (Maskell), comb. nov.
26. Antennae 6-segmented; caudal seta shorter than dorsoapical lobe seta
. *M. nothofagi* (Hoy), comb. nov.
Antennae 7-segmented; caudal seta much longer than dorsoapical lobe seta 27
27. Anal ring with six setae; ventral macrotubular ducts confined to abdominal margins and area between antennae *M. nelsonensis* (Hoy), comb. nov.
Anal ring with eight setae; ventral macrotubular ducts throughout submarginal zone 28
28. Dorsal setae on head and thorax all more or less same size; dorsal derm with conical nodules 29
Dorsal setae on head and thorax of various sizes, some less than half length of others; dorsal derm with rounded nodules 30
29. All dorsal setae on abdomen approximate in size to those on head and thorax, submedial setae present on abdominal segments VI and VII; more than 10 translucent pores on each hind femora
. *M. maskelli* (Hoy), comb. nov.
Dorsal medial pairs of setae on abdominal segments VI and VII much smaller than those elsewhere on body, dorsal submedial setae absent from abdominal segments VI and VII; less than 10 translucent pores on each hind femora
. *M. podocarpus* (Hoy), comb. nov.
30. Dorsal setae truncate, with broad, concave apices
. *M. argentifagi* (Hoy), comb. nov.
Dorsal setae more evenly attenuated, apices appearing blunt or truncate, but not concave
. *M. rubrifagi* (Hoy), comb. nov.

***Madarococcus argentifagi* (Hoy), comb. nov.**

Eriococcus argentifagi Hoy, 1962a: 31, 44–45, fig. 8. Type data: **New Zealand**: South Island, Southland, Purakaunui Falls, on *Nothofagus menziesii*, 11.xi.1958, J. M. Hoy. Holotype and six paratype females, by original designation. Type depository: NZAC.

Acanthococcus argentifagi; Miller & Gimpel, 1996: 598. Change of combination.

Remarks

The Hoy collection includes one slide of a second-instar female with the same data as the holotype, but it is not labelled as a paratype and was not included in the type series. Hoy (1962a) described the adult female of *M. argentifagi* as lacking translucent pores on the hind legs, but translucent pores are present. *Madarococcus argentifagi* is very similar to *M. rubrifagi*. A distinction can be made between the two species on the basis of the apices of the enlarged dorsal setae: truncate, with broad concave apices in *M. argentifagi*, as opposed to blunt or truncate but never with concave apices in *M. rubrifagi*. It is possible these two collections represent a single species. Perhaps the slight

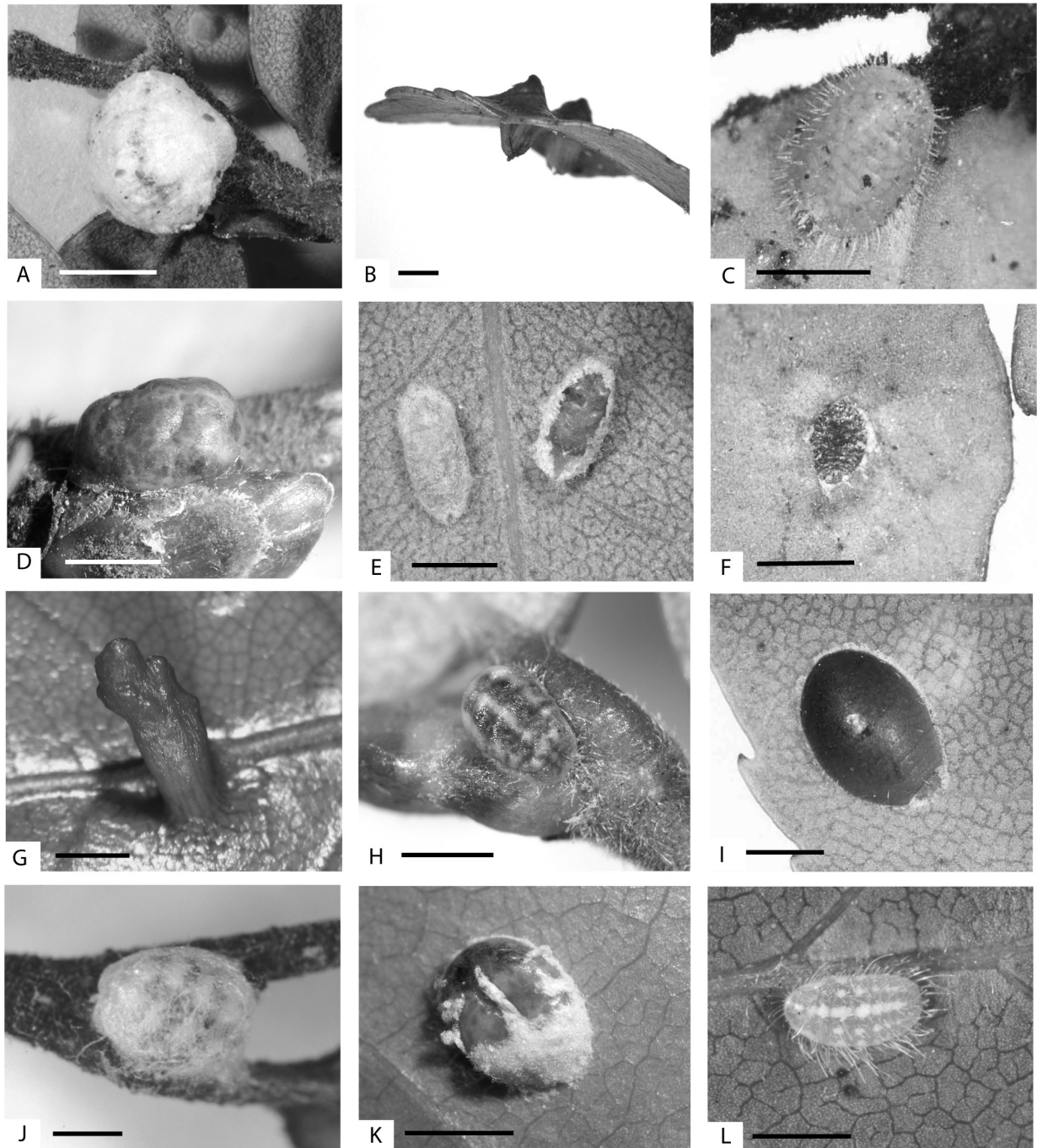


Fig. 4. Adult females of *Madarococcus* spp. in life: *A*, *M. cavellii* with test, on *Nothofagus solandri*; *B*, *M. cucularius*, lateral view of leaf of *N. menziesii* with two pouch galls; *C*, *M. cunninghamii* on leaf base of *N. cunninghamii*; *D*, *M. intermedius*, ex *N. menziesii*, mature female on leaf axil; *E*, *M. maskelli* on leaf of *N. solandri*, two females (one upturned), each with test; *F*, *M. meander*, dorsum flush with abaxial surface of leaf of *N. cunninghamii*, expanded venter occupying gall cavity (not shown); *G*, gall of *M. megaventris* on leaf of *N. moorei*; *H*, *M. montifagi* on *N. solandri*, young female in leaf axil (mature females may feed on leaves); *I*, *M. moorei* on leaf of *N. moorei*, mature specimen (younger females feed in leaf axils); *J*, *M. nelsonensis* in lightly woven test on twig of *N. fusca*; *K*, *M. rotundus* on leaf of *N. fusca*, mature female with distinctive wax pattern; *L*, *M. viridulus* on leaf of *N. fusca*. Scale bars = 1 mm.

morphological variation can be attributed to the effects of feeding on different hosts, *M. argentifagi* on *N. menziesii* and *M. rubrifagi* on *N. fusca*. *Madarococcus argentifagi* is also similar to *M. nelsonensis* and *M. nothofagi* [see comments under *M. nothofagi*]. The adult females of *M. argentifagi* can be distinguished from those of *M. nelsonensis* by 1, lacking quinquelocular pores between hind coxae (several present in *M. nelsonensis*), and 2, having hind legs approximately same size as fore and mid legs (hind legs much larger than fore or mid legs in *M. nelsonensis*). Adult females of *M. argentifagi* differ from those of *M. nothofagi* by having 1, caudal seta longer than dorsoapical lobe seta (caudal seta shorter than dorsoapical lobe seta in *M. nothofagi*) and 2, 7-segmented antennae (6-segmented in *M. nothofagi*).

Madarococcus cavellii (Maskell), comb. nov.

(Fig. 4A)

Gossyparia cavellii Maskell, 1890: 147–149, pl. VII, figs 13–22. Type data: **New Zealand**: North Island, Rimutaka Mountains, near Wellington; South Island, Caplestone, near Reefton; on *N. menziesii* (as *Fagus menziesii*). Lectotype female, by subsequent designation of Deitz & Tocker, 1980: 45. Type depository: NZAC.

Gossyparia cavellii; Fernald, 1903: 68. Misspelling of species name.

Nidularia cavellii; Lindinger, 1933: 108. Change of combination.

Eriococcus cavellii; Hoy, 1962a: 6, 22, 31, 52–53, fig. 12. Change of combination.

Acanthococcus cavellii; Miller & Gimpel, 1996: 599. Change of combination.

Material examined

New Zealand: NN, Nelson, Church Hill, *N. solandri*; KA, Puhipuhi River, *N. ?solandri* (NZAC); MC, Klondyke Corner, in stem axil of *N. solandri* (ANIC); MC, Banks Peninsula, Hinewai Reserve, *N. fusca* stems in leaf bud axils, some with galls (NZAC); MC, Christchurch, Riccarton Rd (lower), *N. fusca* at nodes with stem swelling and *N. solandri* stems at nodes (NZAC); MC, Craigieburn Forest Park, *N. solandri* stems (NZAC); DN, Dunedin, Otago Museum Reserve, [no host] (NZAC); DN, Dunedin, Woodhaugh Gardens, *N. solandri* (NZAC).

Remarks

Hoy (1962a) illustrated and redescribed the adult female of this species. RCH discovered that Maskell's dry material of this species (slide-mounted by Hoy for his 1962a revision) had been a mixed series of both *M. cavellii* and *M. nelsonensis* (Henderson & Martin 2006). Thus there is some uncertainty concerning whether Maskell (1890) and later Hoy (1962a) accidentally described the test of *M. nelsonensis* as if it belonged to *M. cavellii*. Maskell (1890: 147) described the adult female of *E. cavellii* as dark purple in colour and 'resting on a cushion of yellowish or grayish cotton, with filaments of the same more or less sparsely covering the dorsum; sometimes the body of the insect is quite clearly visible through the threads, at others it is scarcely to be seen'. Maskell's description of the wax is consistent with the distribution and density of the macrotubular ducts seen on the dorsum as well as the ventral submargin of the adult female, except that the almost complete covering of some females by their test might be based on *M. nelsonensis*. A further complication is that recent collections by N. A. Martin and RCH show that there is some variation among populations of *M. cavellii* in the

degree of waxy covering and stem distortion caused by the adult female depending on its *Nothofagus* host and its locality. On *N. fusca* at Banks Peninsula, females of *E. cavellii* are naked and sit on a cushion swelling at the stem nodes (Henderson and Martin 2006, Fig. 14), causing the young stems to appear knotty, whereas on *N. fusca* at Christchurch, the females have some cottony covering but cause little stem swelling; on *N. solandri* at Christchurch, females have a white loose covering (Fig. 4A) and no obvious associated stem swelling. Maskell (1890) noted that feeding by females of *M. cavellii* affected the stem axils of *N. menziesii*. It is not known whether the differences described above are host effects or reflect genetic variation among the insect populations. On females from the Banks Peninsula, the dorsal setae are size-restricted anteriorly, perhaps due to 'pressure' of the leaf bud covering that part of the insect, as the female has its head resting against the axil.

Madarococcus cavellii is most easily confused with *M. hispidus*. Both species are characterised by numerous spinose setae on the lateral areas of the venter. This feature is apparent even on the first-instar nymphs of *M. cavellii* (all ventral setae are minute and slender in the first-instar nymphs of *M. hispidus*). The adult female of *M. cavellii* can be distinguished from that of *M. hispidus* by 1, hind coxae much larger than fore or mid coxae (coxae of all legs subequal in *M. hispidus*); 2, majority of ventral disc pores quinquelocular (most disc pores trilocular in *M. hispidus*), and 3, ventral abdominal setae short and robust (longer and flagellate in *M. hispidus*).

Madarococcus chilensis (Miller & González)

Eriococcus chilensis Miller & González, 1975: 140–142, Fig. 4. Type data: **Chile**: Magallanes, Puerto del Hambre, on *N. betuloides*, 18.xii.1971, R. González. Holotype and eight paratype females, by original designation. Type depositories: MEUC; BMNH; USNM.

Material examined

Chile: Parque Nacional Puyehue, Antillanca Ski Resort, on underside of leaves of *N. pumilio* (ANIC, BME).

Remarks

The adult females of *M. chilensis* are very similar to those of *M. navarinoensis* and *M. rhadinotrix*, each having 1, two sizes of quinquelocular pores on the venter; 2, macrotubular ducts on the ventromedial surface of the abdomen that are smaller than those on the dorsum, and 3, dorsoapical anal lobe setae that are closer to or as close to the dorsomedial setae as to the caudal setae. The adult females of *M. chilensis* can be separated from the other two species by the presence of dorsomedial abdominal setae that are approximately the same as the largest marginal setae, however there can be some variation in the lengths of the dorsal setae even among specimens from one locality. The morphological delimitation of these three species given by Miller and González (1975) requires further study.

Madarococcus cruriamplus Hoy

Madarococcus cruriamplus Hoy, 1962a: 151–153, fig. 61. Type data: **New Zealand**: South Island, Maruia Springs, on *Nothofagus* sp., 10.xi.1935, G. Brittin; Maruia, on *Nothofagus* sp., xii.1935,

G. Brittin. Holotype and four paratype females, by original designation. Type depository: NZAC.

Material examined

New Zealand: BR, Alfred River, Lake Daniells Track, *N. fusca* leaves (NZAC).

Remarks

Madarococcus cruriamplis appears to be closely related to *M. maculatus* [see comments under *M. maculatus*]. The adult females are green in life and lack a test.

Madarococcus cunicularius Hoy

(Fig. 4B)

Madarococcus cunicularius Hoy, 1962a: 151, 154–155, 204, fig. 62.

Type data: **New Zealand:** North Island, Rangataua, on *N. menziesii*, 08.ii.1960, J. M. Hoy. Holotype and 15 paratype females, by original designation. Type depository: NZAC.

Material examined

New Zealand: NN, Golden Downs, leaf galls on *N. menziesii* (NZAC); NN, Korere-Tophouse Road, near Tophouse T-junction, leaf galls on *N. menziesii* (NZAC); BR, near St Arnaud, Mt Robert, leaf galls on *N. menziesii* (ANIC).

Remarks

Hoy (1962a) provides an additional host record: G. Brittin collected *M. cunicularius* from *N. fusca*. The adult female of *M. cunicularius* is pale yellow in colour and completely encased in its gall (Fig. 4B) with an irregular abaxial opening formed by striated, finger-like projections of host tissue. The gall is described and illustrated by Henderson and Martin (2006). *Madarococcus cunicularius* most closely resembles *M. meander*, sp. nov., which induces open-pit galls, although the molecular data do not support a sister-group relationship between these two species. For discussion of the morphological similarities of *M. cunicularius* and *M. meander*, sp. nov. see comments under *M. meander*, sp. nov.

Madarococcus cunninghamii Hardy & Gullan, sp. nov.

(Figs 4C, 5, 6)

Madarococcus sp.: McQuillan, 1993: 349 (as undescribed).

Material examined

Holotype. Tasmania: 1 adult female: Ridgley, 41°10'S, 145°50'E, on leaf of ornamentally planted tree of *N. cunninghamii*, 29.i.1996, D. W. deLittle (ANIC).

Paratypes. **Tasmania:** 6 adult females, 1 second-instar female and c. 30 first-instar nymphs (three slides): same data as holotype (ANIC); 9 adult females and 4 first-instar nymphs (one slide): same data as holotype except 17.i.1996 (ANIC); 2 adult females: Collinsvale, 500 m, 2.v.1981, M. Williams, 50 B6, Record 69893 (TASAG); 18 adult females: Davis Creek, 39 miles [63 km] E of Queenstown, on *N. cunninghamii*, 27.vi.1971, J. W. Beardsley (BPBM); 3 adult females: Fern Tree, on *N. cunninghamii*, 21.i.1962, N. M. Hudson (BMNH); 9 adult females (five slides): Hellyer's Gorge, on leaf of *Nothofagus*, [no date], J. M. Cox # 275 (BMNH); 17 adult females (four slides): 20 miles [32 km] W of Maydena, on *N. cunninghamii*, 26.vi.1972, J. W. Beardsley (BPBM); 10 adult females: Meander State Forest, picnic area, 41°43'03''S, 146°34'04''E, on leaves of *N. cunning-*

hamii, 24.i.2006, PJG (six slides ANIC, two slides TASAG, two slides USNM); 4 adult females: Mt Barrow, on leaf of *Nothofagus*, 17.ii.1973, J. M. Cox #279 (BMNH); 3 adult females: Mt Field N.P., information centre, on leaves of *N. cunninghamii*, 7.ii.1992, PJG and T. K. Qin (ANIC); 13 adult females: Mt Field N.P., 42°40'17''S, 146°40'50''E, on leaves of *N. cunninghamii*, 23.i.2006, PJG (seven slides ANIC, three slides TASAG, three slides USNM); 1 adult female and 5 embryos: Mt Field N.P., Lyrebird Walk, 680 m, ex *N. cunninghamii*, 10.iv.2000, P. J. Keble-Williams, HeEr1 (TASAG); 1 adult female: c. 2 km N of St Columba Falls, 41°18'39''S, 147°56'02''E, on leaf of *N. cunninghamii*, 26.i.2006, PJG (ANIC); 3 adult females: near Strahan, 28.vi.1972, J. W. Beardsley (BPBM); 4 adult females (two slides): Tahune Forest Park, on *N. cunninghamii*, 18.xi.1978, M. A. Williams (BMNH); 3 adult females: 10 km SSE of Weldborough, 41°13'S, 147°56'E, ex leaves of *N. cunninghamii*, 26.i.2006, PJG (ANIC). **Victoria:** 6 adult females (two slides): Donna Buang, on *N. sp.*, 3.xi.1963, S. W. Brown (ANIC); 13 adult females (13 slides): 8 or 10 miles [13 or 32 km] E of Marysville, on *N. cunninghamii*, 19.x.1971, J. W. Beardsley (BPBM); 1 adult female and 1 second-instar male (one slide) and 1 second-instar male and 1 first-instar nymph (one slide): Otway Ranges, at base of leaf underside on *N. cunninghamii*, 27.x.1971, J. W. Beardsley, V-162 (BPBM).

Description

Adult female (Fig. 5)

Live material. Occurring on underside of leaf near petiole (Fig. 4C). Body colour bright green, some specimens with longitudinal bands of brown cuticle, others with dorsum entirely brown. Glassy filaments (maximum length 0.2–0.3 mm) born on enlarged setae, projecting dorsally and marginally.

Mounted material. Body outline ovate to subcordate, length 0.96–2.25 mm (holotype 1.70 mm), greatest width 0.58–1.80 mm (holotype 1.34 mm). Eyespot on or just dorsad of margin, 15–20 µm wide. Antennae 6-segmented; length 100–155 µm; with three hair-like setae (trichoid sensilla) on segment I, two hair-like seta on II, two hair-like seta on III, one fleshy seta on IV, three hair-like setae and one fleshy seta on V, and c. six hair-like setae plus three fleshy setae on VI. Frontal (interantennal) lobes present, sometimes difficult to detect. Tentorial box 100–112 µm long, 98–112 µm wide. Labium 50–62 µm long, 60–82 µm wide; basal segment lost, apical two segments fused; five pairs of setae on anterior surface, one pair of setae on posterior surface, and one apical pair of short setae. Spiracles 32–42 µm long, 13–20 µm wide across atrium. Legs increasing in size caudad; fore legs: coxa 32–40 µm, trochanter + femur 100–107 µm, tibia 40–60 µm, tarsus 62–70 µm; mid legs: coxa 35–42 µm, trochanter + femur 102–120 µm, tibia 45–55 µm, tarsus 65–72 µm; hind legs: coxa 50–62 µm, trochanter + femur 105–130 µm, tibia 47–60 µm, tarsus 75–85 µm; claw 15 µm long; fore coxa with six setae, mid and hind coxa each with five setae, trochanter and femur with four setae (long seta on trochanter 47–50 µm), tibia with three setae, and tarsus with five setae; tarsal digitules 21–28 µm long; claw digitules unequal 16–19 µm long, one with apical knob 6 µm wide, other with apical knob 2 µm wide; translucent pores on both surfaces of hind coxa and femur, dorsal and ventral surfaces of hind coxa each with c. 50 pores, dorsal and ventral surfaces of hind femur with c. 20 and 10 pores respectively. Anal ring 50–64 µm wide, bearing eight setae, 120–170 µm long. Suranal setae spatulate, 70–85 µm long. Anal lobes subclavate, with distal portion of inner margin crenulate, invested with ~10 microtubular ducts; ventral lobe seta 15–25 µm, dorsolateral

just ventrad of marginal fringe; setae medial of coxae 30–45 µm long; setae on head posteromedial of antennal insertions 32–45 µm long. Macrotubular ducts 13–15 µm long, only two pairs, posterolateral of vulva. Microtubular ducts absent. Quinquelocular pores 4 µm in diameter, clustered in submedial band extending from anal ring to posterior spiracles, then continuing from anterior spiracles to bases of antennae, pores absent from space between anterior and posterior spiracles (except possibly for pores near long setae anteromedial of mid coxae).

Diagnostic features

Madarococcus cunninghamii would be most easily confused with *M. pulchellus* or *M. viridulus*. In life, the adult females of all three species are light green and extrude glassy filaments from enlarged dorsal setae (Fig. 4C, L). The slide-mounted adult females of these three species are similar in lacking macrotubular ducts on the dorsum, and having only enlarged dorsal setae. *Madarococcus cunninghamii* can be recognised by having 1, macrotubular ducts present posterolateral of the vulva; 2, apical lobe seta shorter than dorsoapical lobe seta, and 3, a 2-segmented labium.

First-instar nymph (Fig. 6)

Mounted material. Body length 300–342 µm, greatest width 145–235 µm. Eyespot on margin, 8–10 µm wide. Antennae 6-segmented, 69–73 µm long; with three hair-like setae (trichoid sensilla) on segment I, one hair-like seta on II, two hair-like setae on III, one fleshy seta on IV, three hair-like setae and one fleshy seta on V, and ~6 hair-like setae plus three fleshy setae on VI. Tentorial box 57–62 µm long, 49–60 µm wide. Labium composed of two fused segments, c. 30 µm long, 32–40 µm wide; with five pairs of setae on anterior surface, one pair of short apical setae, and one pair of setae on posterior surface. Spiracles 10–12 µm long, 5 µm wide across atrium. All legs more or less same size; coxa 12–16 µm, trochanter + femur 52–56 µm, tibia 22–27 µm, tarsus 30–37 µm, claw 9–11 µm; tarsal digitules unequal 12–20 µm; claw digitules 10–13 µm long, asymmetrical, one with terminal knob 2 µm wide, the other with terminal knob 1 µm wide. Anal ring 18–21 µm wide, bearing six setae, 35–40 µm long. Suranal setae spatulate, 24–26 µm long, arising from small pad of sclerotic cuticle. Anal lobes subconic, 25–27 µm long, inner margin crenulate; ventral lobe seta 11–14 µm, dorsolateral lobe seta 7–9 µm, dorsomedial lobe seta 9–11 µm, dorsoapical lobe seta 27–33 µm, caudal seta 23–35 µm.

Dorsum dominated by three pairs of greatly enlarged, spinose setae, arising from submedial portion of metathorax, prothorax and anterior margin of head (these setae of same size and shape as those on dorsum of adult females); each seta 27–54 µm long, with blunt apex and swollen base; short (each 2 µm long), blunt-tipped setae in two longitudinal rows on each side of body: one medial series on each side of body running from abdominal segment VII to metathorax, and one submedial series on each side of body extending from anterior abdominal segments to prothorax. Margin with distinct fringe of setae, each seta 15–20 µm long, similar to enlarged dorsal setae, with one seta on each side of each abdominal segment, two setae on each side of both metathorax and mesothorax, five setae on each side

of both prothorax and head. Macrotubular ducts absent. Microtubular ducts 5–8 µm long, one anterior to each anal lobe, others associated with about half of marginal fringe setae and with each enlarged dorsal seta.

Venter with setae in three longitudinal rows on each side of abdomen, one marginal and one submarginal row on each side of body extending onto mesothorax; each seta 3–10 µm long, setae medial of coxae difficult to detect, 10–15 µm long; three pairs of setae on head between antennal insertion points, each seta 11–32 µm long. Macrotubular ducts and microtubular ducts absent. Trilocular pores arranged in a single longitudinal row on each side of abdomen, between medial and submarginal rows of setae; one near each posterior spiracle, two near each anterior spiracle, pores medial of coxae not detected.

Diagnostic features

The three pairs of enlarged dorsal setae are unique amongst the first-instar nymphs of known eriococcids on *Nothofagus*.

Remarks

Despite the superficial similarity between the adult females of *M. cunninghamii* and those of the New Zealand species *M. viridulus* and *M. pulchellus*, the sequence data strongly support (PP = 1.0) a sister-group relationship between *M. cunninghamii* and the Australian species *M. moorei*, sp. nov.

Etymology

This species is named for its host *N. cunninghamii*.

Madarococcus detectus (Hoy), comb. nov.

Eriococcus detectus Hoy, 1962a: 70–71, fig. 21. Type data: **New Zealand:** South Island, Christchurch, on *N. solandri* var. *solandri*, 16.xii.1915, G. Brittin. Holotype and five paratype females, by original designation. Type depository: NZAC.

Acanthococcus detectus; Miller & Gimpel, 1996: 600. Change of combination.

Remarks

Hoy (1962a) erroneously described the adult female of *M. detectus* as having dorsal macrotubular ducts, but macrotubular ducts are confined to marginal and submarginal zones of the venter. *Madarococcus detectus* appears to be most closely related to *M. montifagi*, with both species having a rotund body shape, lacking dorsal macrotubular ducts and having a conspicuous pit near the anterior margin of the dorsal surface of each anal lobe. *Madarococcus detectus* is easily distinguished from *M. montifagi* by having several enlarged dorsal setae (*M. montifagi* has only minute setae on the dorsum).

Madarococcus eurythrix (Miller & González), comb. nov.

Eriococcus eurythrix Miller & González, 1975: 142–144, Fig. 5. Type data: **Chile:** near Villa Portales, on *Nothofagus antarctica*, 25.xi.1968, R. González. Holotype and 26 paratype females, by original designation. Type depositories: Holotype: MEUC; Paratypes: BMNH, NZAC, MNHM, BME, USNM (including VIP), ZIN.

Acanthococcus eurythrix; Miller & Gimpel, 1996: 600. Change of combination.

Material examined

Chile: IX Region, Villarrica, leaves of *N. alpina* (ANIC, BME); same data as previous but leaf of *N. obliqua* (ANIC); X Region, Hotel Peulla, ex leaves of *N. obliqua* (BME).

Remarks

We have examined specimens from four locations in Chile on *N. alpina*, *N. antarctica* and *N. obliqua*. *Madarococcus eurythrix* bears several morphological similarities with the Chilean species *M. chilensis*, *M. navarinoensis*, and *M. rhadinothrix*: 1, slender,

slightly curved dorsal setae; 2, a loose marginal fringe of enlarged setae, most distinct on posterior abdominal segments, becoming staggered on thorax and head, and 3, dorsal setae without associated microtubular ducts. *Madarococcus eurythrix* also shares some key features with the Australasian *Madarococcus* species: 1, spatulate suranal setae; 2, interantennal lobes; 3, ventral macrotubular ducts of a single size, similar to those on dorsum, and 4, disc pores of a single size (two sizes of disc pores are found on the ventral surfaces of *E. chilensis*, *E. navarinoensis* and *M. rhadinothrix*). *Madarococcus eurythrix*

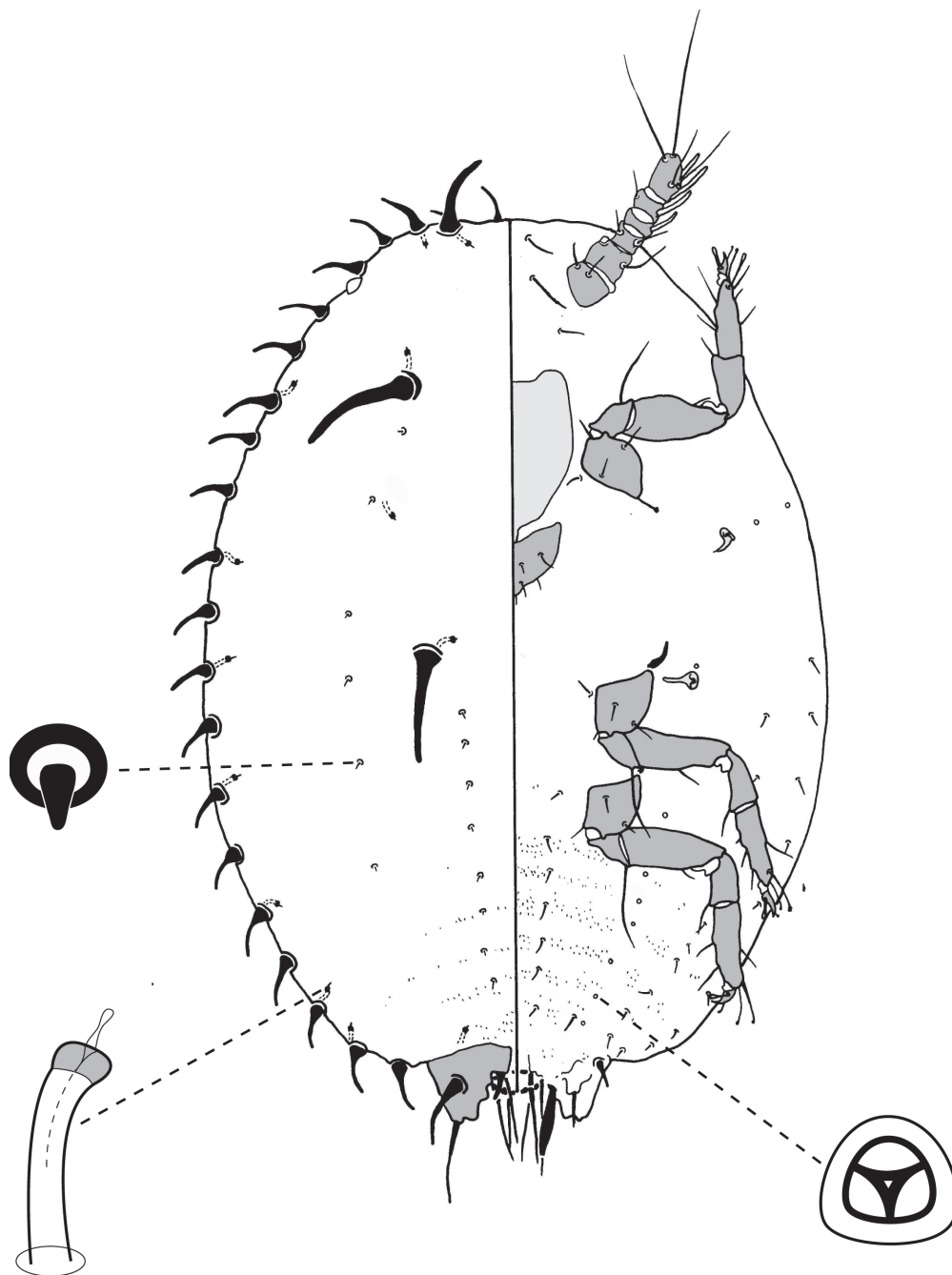


Fig. 6. First-instar nymph of *Madarococcus cunninghamii*, sp. nov.

most closely resembles the Tasmanian species *M. occultus*, sp. nov. Characteristics shared by these two species include 1, the shape and distribution of the dorsal and marginal setae; 2, anal lobes small in comparison to those of other *Madarococcus* species, and 3, macrotubular ducts present on the medial portions of each abdominal segment. In our analysis of the sequence data, we found weak support (PP = 0.87) for a clade comprised of *M. eurythrix* along with two other Chilean *Madarococcus* populations, *M. navarinoensis* and *M. nr navarinoensis*.

Madarococcus fagicorticis (Maskell), comb. nov.

Eriococcus fagicorticis Maskell, 1892: 27, pl. V, figs 1–5. – Hoy, 1962a: 76, fig. 24. Type data: **New Zealand**: South Island, Reefton district, on *N. fusca* (as *Fagus fusca*). Lectotype female, by subsequent designation of Deitz & Tocker, 1980: 46. Type depository: NZAC. *Nidularia fagicorticis*; Lindinger, 1933: 108. Change of combination. *Acanthococcus fagicorticis*; Miller & Gimpel, 1996: 600. Change of combination.

Remarks

Hoy (1962a) illustrated and redescribed the adult female of this species. Miller and Gimpel (2000) incorrectly list York Bay as part of the type data. In his list of specimens examined, Hoy (1962a) clearly states that one specimen from York Bay was collected by D. Miller in 1922; thus it is not part of the type series. Unfortunately the lectotype female of this species was lost during curatorial remounting. There is some probable paralectotype material in the NZAC: 1, a slide with one adult female and the data: ‘*Eriococcus fagicorticis* / Maskell spare material / X *Nothofagus* / June 1939’ [date of Brittin’s slide-mount] and 2, a Maskell original of a neonate 1st-instar nymph labelled: ‘*Eriococcus fagicorticis* / larva / 1890 / W.M.M.’. We have examined a single specimen from York Bay. It is in poor condition, but appears to match Hoy’s (1962a) illustration. An additional three adult females, on one slide held in the NZAC with the data ‘Lichen on *Nothofagus* sp. / Lake Sylvester / Nelson / 29.iv.69 / J. E. Tobler,’ are in good condition and closely match Hoy’s drawing and description. Thus there is no doubt as to the identity of the species. Maskell (1892) observed that adult females occurred in bark crevices of *N. fusca*, accompanied by a great deal of sooty mould. *Madarococcus fagicorticis* is the only species of *Madarococcus* for which the adult female both produces a test and has a distinct marginal fringe of enlarged setae. The combination of dorsal macrotubular ducts and a marginal fringe make this species easy to distinguish from all other Australasian species.

Madarococcus hispidus (Hoy), comb. nov.

Eriococcus hispidus Hoy, 1962a: 30, 86–87, fig. 29. Type data: **New Zealand**: North Island, Ohakune, on *N. solandri* var. *cliffortioides*, 10.ii.1960, J. M. Hoy. Holotype female, by original designation. Type depository: NZAC. *Acanthococcus hispidus*; Miller & Gimpel, 1996: 601. Change of combination.

Material examined

New Zealand: BP, Te Koau, *N. solandri* (NZAC); BP, East Cape, Rereauira Swamp, Beech Ridge, *N. truncata* (NZAC); GB, Kakanui *N. truncata* (NZAC).

Remarks

Madarococcus hispidus is most similar to *M. cavellii* [see comments under *M. cavellii*].

Madarococcus intermedius (Maskell), comb. nov.

(Fig. 4D)

Rhizococcus intermedius Maskell, 1891: 19–20, pl. V, Figs 8–11. Type data: **New Zealand**: South Island, Reefton, on *N. menziesii* (as *Fagus menziesii*), iii.1890, W. M. Maskell. Lectotype female, by subsequent designation of Deitz & Tocker, 1980: 47. Type depository: NZAC (see below).

Nidularia intermedius; Lindinger, 1933: 116. Change of combination.

Sisyrococcus intermedius; Hoy, 1962a: 182–183, fig. 73. Change of combination.

Material examined

New Zealand: WO, Hamilton Gardens, leaf buds/stunted or aborted shoots of *N. menziesii* (NZAC); TO, Ohakune, Moore St, leaf axils of *N. menziesii* (ANIC); BR, Mai Mai Valley Rd, buds and leaf axils of *N. menziesii* (ANIC); WD, Haast Valley, Pleasant Flat, buds of *N. menziesii* (ANIC).

Remarks

Hoy (1962a) transferred this species as the type of his new genus *Sisyrococcus*, and illustrated and redescribed the adult female. In addition to the lectotype, the NZAC has 1, three original slides: one labelled ‘larva’; one labelled ‘female 2nd-stage’ [actually an adult female]; one labelled ‘2 males’, and 2, 16 slides mounted by Hoy, 14 labelled ‘Mask Coll. / Ex *Nothofagus menziesii* leaf axils / 1890 [no coll no.]’, and two with same data except for a more specific date, March 1890. In addition, Deitz and Tocker (1980) refer to three subsequent slides in the USNM and the entry for this species in ScaleNet (Ben-Dov *et al.* 2007) and the recent world catalogue of Eriococcidae (Miller and Gimpel 2000) refers to ‘Type material also in USNM’. Apparently there is only one USNM slide labelled as ‘*Rhizococcus intermedius* Maskell, New Zealand, Maskell Collection # 124.’ (D. R. Miller personal communication). There are no specimens with the number 124 in the Maskell collection in the NZAC and the type status of the USNM specimen is uncertain.

Hoy’s two species of *Sisyrococcus*, now *M. intermedius* and *M. papillosus*, have very unusual adult females. In mature specimens (Fig. 4D), the dorsal surface of the anterior abdominal segments is folded back and over the posterior segments, concealing the anal lobes from the dorsal aspect. Macrotubular ducts are found only on the dorsal surface of the abdomen and, on the anterior segments, they are arranged in tight, transverse rows. *Madarococcus intermedius* can be distinguished from *M. papillosus* by having far fewer dorsal setae, and all but a few pairs confined to the margin (in *M. papillosus* the dorsum is covered with *c.* 500 setae and the margin is indistinguishable). *Madarococcus intermedius* is unique among *Madarococcus* species in having quinquelocular disc pores on the dorsum, in a narrow medial band on the head. The suranal setae on *M. intermedius* and *M. papillosus* often appear non-spatulate, and in young adult females they can have fine flagellate tips that later break off.

In life, young females of *M. intermedius* are pinkish-brown to pale yellow, whereas adult females are orange-yellow to orange-brown or sometimes reddish or greenish, with short, glassy marginal wax filaments (each emanating from a marginal seta) and a scattering of white wax specks on the dorsum. Mature females shelter embryos in a cavity under their body. Tests of males are creamy white and occur on the undersides of leaves, especially near the leaf margins.

***Madarococcus latilobatus* (Hoy), comb. nov.**

Eriococcus latilobatus Hoy, 1962a: 31, 94–95, fig. 33. Type data: **New Zealand**: South Island, Lake Wakatipu, Lumberbox Creek, on *N. solandri* var. *cliffortioides*, 15.xi.1958, J. M. Hoy. Holotype and five paratype females, by original designation. Type depository: NZAC.

Acanthococcus latilobatus; Miller & Gimpel, 1996: 601. Change of combination.

Remarks

The adult females of *M. latilobatus* most closely resemble those of *M. rotundus*. Hoy (1962a) separated them by counting enlarged dorsal setae: 10–20 on the head and thorax of *M. latilobatus* as opposed to four or fewer located on the thorax of *M. rotundus*. He acknowledges the plasticity of the feature in *M. rotundus*; in many specimens the enlarged setae are completely absent. Setal number may be variable within some species, for example, there is drastic variation in the number of dorsal enlarged setae amongst individuals of *M. moorei*, sp. nov. both within and among separate collections. Perhaps *M. latilobatus* and *M. rotundus* are the same species, but we have insufficient material to investigate this possibility.

***Madarococcus maculatus* (Maskell)**

Rhizococcus maculatus Maskell, 1890: 144–145, pl. VII, figs 6–12. Type data: **New Zealand**: South Island, Reefton district, on *N. solandri* var. *cliffortioides* (as *Fagus cliffortioides*), W. M. Maskell. Lectotype female, by subsequent designation of Deitz & Tocker, 1980: 47. Type depositories: NZAC, USNM (see below).

Nidularia maculatus; Lindinger, 1933: 116. Change of combination.

Madarococcus maculatus; Hoy, 1962a: 6, 7, 151, 156–157, fig. 63. Change of combination.

Material examined

New Zealand: BP, East Cape, Rereauira Swamp, Beech Ridge, *N. truncata* (NZAC); NN, Harwoods Hole, *N. fusca*, females without a sac (NZAC); BR, Springs Junction, Palmer Road, *N. fusca*, females without a test (NZAC).

Remarks

Hoy (1962a) illustrated and redescribed the adult female of this species and provided *N. fusca* as an additional host record based on a collection from Ohakune. Although Hoy admits that his description of the adult female conflicts with that of Maskell (1890), he based it on the only available material identified by Maskell as *Rhizococcus maculatus*. Maskell's label on the lectotype female is 'Rhizococcus maculatus / female - 2nd stage / on Fagus sp. / Sept. 1889 W.M.M.' but this female is adult as indicated by Hoy's subsequent label: '*Madarococcus maculatus* / adult female / det. J. M. Hoy 1961'. Another Maskell slide sim-

ilarly labelled as 'early 2nd stage' is not *M. maculatus* and a third Maskell slide with this species name has four first-instar nymphs. If the second-instar described by Maskell was, in fact, an adult, his and Hoy's description differ only in the number of antennal segments (six according to Maskell v. seven according to Hoy). More conflict arises when Hoy's description is compared to Maskell's description of the adult female, in which Maskell asserts that no dorsal spines are present, whereas Hoy counts c. 28. Perhaps the 'adult' of Maskell was an older specimen in which the dorsal setae had been damaged or lost.

There is some probable paralectotype material in the USNM but the status of Maskell material sent to the USA is uncertain. The one slide-mounted USNM specimen, with Maskell No. 112, was mounted subsequently (not by Maskell) but may have been part of the series that Maskell used to describe the species; the Cockerell Collection in the USNM also has dry material identified as this species, with Maskell No. 56 (D. R. Miller personal communication). There is no Maskell material in the NZAC with the numbers 56 or 112.

The adult females of *M. maculatus* are most similar to those of *M. cruriamplus*. Features shared between the two are: 1, macrotubular ducts absent; 2, enlarged dorsal setae few or absent; 3, distinct marginal fringe present, and 4, suranal setae approximately as long as anal lobes. The adult females of *M. maculatus* differ from those of *M. cruriamplus* by having numerous enlarged dorsal setae (all dorsal setae minute in *M. cruriamplus*).

***Madarococcus maskelli* (Hoy), comb. nov.**

(Fig. 4E)

Eriococcus maskelli Hoy, 1962a: 98–99, fig. 35. Type data: **New Zealand**, on *N. solandri* var. *cliffortioides*. Holotype and five paratype females, by original designation. Type depository: NZAC.

Acanthococcus maskelli; Miller & Gimpel, 1996: 602. Change of combination.

Material examined

New Zealand: NN, Inwoods Lookout, *N. menziesii*, underside leaves, in tawny tests (NZAC); MC, Lake Pearson, State Highway 73, forest by roadside, *N. solandri* underside leaves (NZAC); FD, Lake Manapouri, Spey River flats, *N. menziesii* (NZAC).

Remarks

No type data, other than the country and host plant, are available. The type specimens came from Maskell's duplicate material and were labelled as *Eriococcus raithbyi* (Hoy, 1962a). *Madarococcus maskelli* is very similar to *M. podocarpi*. Both species have dorsal nodules with acute apices, a feature unique among species of *Madarococcus* except *M. fagicorticis*. A distinction between the two species can be made on the basis of the dorsal setae on the posterior abdominal segments. In *M. maskelli* all dorsal setae are approximately the same size, and the submedial areas on each side of each of segments VI and VII are occupied by one or more setae. In *M. podocarpi*, abdominal segments VI and VII have the medial pairs of setae much smaller than those on the rest of the dorsum, and the submedial areas are without setae. The medial setae on last three abdominal segments of the type specimens of *E. maskelli* are 18–25 µm

long, whereas the same setae on the holotype of *E. podocarp* are 3–5 μm long. Also, adult females of *M. maskelli* usually have more translucent pores on the hind coxa and femur than females of *M. podocarp*, but this variation needs to be verified in a larger sample of specimens.

Recent collections of adult females of *M. maskelli* on *N. solandri* (MC, Lake Pearson, #05–167, 5 females) match the types in that the medial dorsal setae on the last three abdominal segments are about the same size as those on the head, whereas the medial dorsal setae on the last three abdominal segments are smaller than those on the head on three specimens from *N. menziesii* (NN, Inwoods Lookout, and FD, Lake Manapouri).

***Madarococcus meander* Hardy & Gullan, sp. nov.**

(Figs 4F, 7, 8)

Material examined

Holotype. Tasmania: 1 adult female: Meander Forest Reserve, Mother Cummings Creek, ex pit gall on under leaf of *N. cunninghamii*, 12.xi.1999, PJG (ANIC).

Paratypes. **Tasmania:** 4 adult females and c. 30 first-instar nymphs (three slides): same data as holotype (six slides ANIC, one slide TASAG); 1 adult female: Meander State Forest, 19.ii.2004, ex pit gall on leaf of *N. cunninghamii*, L. G. Cook & M. D. Crisp (ANIC); 4 adult females: Cradle Mountain-Lake St Clair N.P., Dove Lake, 41°39'37''S, 145°57'27''E, 950 m, ex pit galls on leaves of *N. cunninghamii*, 25.i.2006, PJG (two slides ANIC, two slides TASAG); 1 adult female: Mt Field N.P., 42°40'17''S, 146°40'50''E, ex pit gall on leaf of *N. cunninghamii*, 23.i.2006, PJG (ANIC); 4 adult females: near Strahan, on *N. cunninghamii*, 28.vi.1972, J. W. Beardsley (BPBM); 4 adult females: 10 km SSE of Weldborough, 41°13'S, 147°56'E, ex pit galls on underside of leaves of *N. cunninghamii*, 26.i.2006, PJG (three slides ANIC, one slide USNM). **Victoria:** 11 adult females (seven slides): 8 miles [13 km] E of Marysville, in small pit or leaf pocket galls on leaves of *N. cunninghamii*, 19.x.1971, J. W. Beardsley, V-134 (BPBM); 3 adult females (one slide): Otway Ranges, 27.x.1972, ex pit galls in leaves of *N. cunninghamii*, J. W. Beardsley, V-162 (BPBM).

Description

Adult female (Fig. 7)

Live material. The female of *M. meander* induces a small pit gall on the leaves of *N. cunninghamii* (Fig. 4F). The body of the female fills the leaf pit, with the female's dorsum lying level with the top of the pit and becoming more sclerotized with age. White wax is extruded from between the anal lobes and around the margin of the body. The colour of the live female is yellow-brown, becoming darker with age. The female is ovoviparous and newly emerged crawlers do not shelter under female's body before dispersing.

Mounted material. Body outline ovate, length 0.88–1.28 mm (holotype 1.26 mm), greatest width 0.70–1.14 mm (holotype 0.94 mm), venter slightly larger than dorsum in more fully expanded specimens. Eyespot 15–17 μm wide, ventrad of margin. Antennae 6-segmented; length 85–102 μm ; with four hair-like setae (trichoid sensilla) on segment I, 2–3 hair-like seta on II, two hair-like setae on III, one fleshy seta on IV, 3–4 hair-like setae plus one fleshy seta on V, and seven hair-like seta plus three fleshy seta on VI. Frontal (interantennal) lobes not detected. Tentorial box 75–85 μm long, 70–75 μm wide. Labium

50–80 μm long, 42–50 μm wide; 3-segmented; seven pairs of seta on anterior surface, one apical pair of short setae, one pair of seta on posterior surface. Spiracles 20–25 μm long, 10 μm wide across atrium. Legs subequal (except hind tarsi that are 5–11 μm longer than mid tarsi or fore tarsi); coxa 22–35 μm , trochanter + femur 70–87 μm , tibia 32–42 μm , tarsus 45–62 μm , claw 15 μm ; coxa with six setae, trochanter with four setae (longest seta 30–40 μm), fore femur with six setae, mid femur and hind femur each with five setae, tibia with four setae, tarsus with six setae; tarsal digitules 22–27 μm long, claw digitules dissimilar, 15–20 μm long, one with apical knob 4 μm wide, other with apical knob 1 μm wide; hind coxa with c. 15 translucent pores on dorsolateral surface. Anal ring 30–35 μm wide, bearing six setae, 60–75 μm long. Suranal setae spatulate, 17–20 μm long. Anal lobes 47–61 μm long, with inner margin parallel to longitudinal body-axis, each lobe with one microtubular duct; ventral lobe seta 13–17 μm long, spatulate, dorso-lateral lobe seta 26–33 μm , dorsomedial lobe seta 26–38 μm , dorsoapical lobe seta 29–39 μm , caudal seta 70–71 μm .

Dorsum. Derm sclerotic. Dorsal setae 1–7 μm long, squat, spinose; one medial pair on each segment except prothorax with two pairs, and abdominal segment VIII with no setae; one sub-medial seta on each side of abdominal segment I and head; 2–3 setae in transverse row extending laterad of each medial seta on thoracic segments. Margin delineated by fringe of slightly curved setae, 18–37 μm long; one seta on each side of abdominal segments II–VII, two setae on each side of abdominal segment I, three setae on each side of metathorax and three setae on each side of mesothorax, continuous series of ~11 setae on each side of prothorax and head, fringe deflected dorsad over eyes. Macrotubular ducts 10–12 μm long, in marginal series. Microtubular ducts ~5 μm long, a single medial duct on abdominal segment VIII.

Venter. Flagellate setae 6–15 μm long, in a transverse row across each abdominal segment; setae medial of coxae 8–20 μm long, setae on head between antennae 11–35 μm long. Macrotubular ducts absent. Microtubular ducts confined to sub-margin of posterior abdominal segments, one duct on each side of abdominal segments V–VII. Quinquelocular pores 3 μm in diameter, scarce; in linear series running from anal lobes to posterior spiracles, clustered around anterior and posterior spiracles, 1–2 medial of each coxa.

Diagnostic features

Madarococcus meander is most similar to the other gall-inducing *Madarococcus* species, *M. cunicularius* and *M. megaventris*, sp. nov. All three species have 1, 6-segmented antennae; 2, a sclerotic dorsum; 3, relatively few dorsal setae; 4, an expanded venter, and 5, no ventral tubular ducts. Adult females of *M. meander* and *M. cunicularius* can be distinguished from those of *M. megaventris*, sp. nov. by having 1, spatulate suranal setae (evenly attenuated in *M. megaventris*, sp. nov.); 2, ventral lobe seta arising proximal of caudal seta (arising distal of apical seta in *M. megaventris*, sp. nov.); 3, relatively few dorsal tubular ducts (numerous in *M. megaventris*, sp. nov.), and 4, venter only moderately expanded (extremely expanded in *M. megaventris*, sp. nov.). Adult females of *M. meander* can be distinguished from adult females of *M. cunicularius* by having 1, macrotubular ducts along the margin (in *M. cunicularius* macrotubular ducts are

completely absent); 2, far fewer disc pores on the ventral surface of the abdomen (only a sparse submedial line as opposed to a broad submedial longitudinal band), and 3, a distinctive anal lobe shape: truncate apex and straight inner margin parallel to the longitudinal body-axis (the anal lobes of *M. cunicularius* are subconical and have rounded apices).

First-instar nymph (Fig. 8)

Mounted material. Body length 300–415 μm , greatest width 127–220 μm . Eyespot 9–11 μm wide, on margin. Antennae 6-segmented, 56–68 μm long; with three hair-like setae (trichoid sensilla) on segment I, two hair-like setae on II, two hair-like seta on III, one fleshy seta on IV, three hair-like

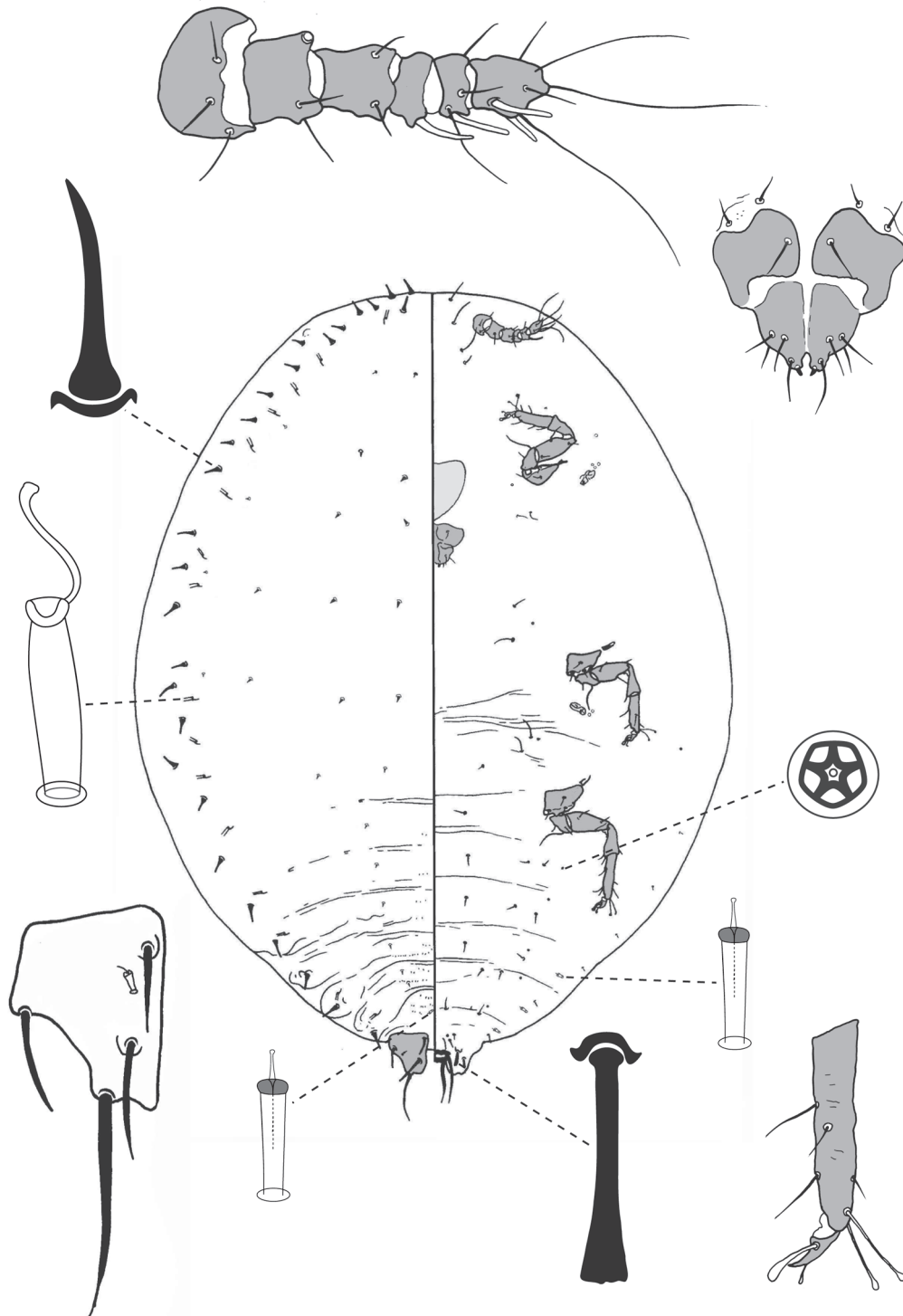


Fig. 7. Adult female of *Madarococcus meander*, sp. nov.

setae plus one fleshy seta on V, and seven hair-like setae plus three fleshy seta on VI. Tentorial box 52–60 μm long, 50–58 μm wide. Labium 3-segmented, 27–36 μm long, 30–38 μm wide; seven pairs of setae on anterior surface, one apical pair of short setae, one pair of setae on posterior surface. Spiracles 12–16 μm long, 5–6 μm wide across atrium. Legs subequal; coxa 12–17 μm , trochanter + femur 47–51 μm , tibia 18–27 μm , tarsus 27–38 μm , claw 10–12 μm ; tarsal digitules 15–19 μm long, claw digitules 10–13 μm long, one more robust than other. Anal ring 20 μm wide, bearing six setae, 31–38 μm long. Suranal setae spatulate, 13–15 μm long. Anal lobes 22–32 μm long, subconic; ventral lobe seta spatulate, 10–13 μm long, dorsolateral lobe seta 9–12 μm , dorsomedial lobe seta 14–17 μm , dorsoapical lobe seta 19–21 μm , apical seta 37–50 μm .

Dorsum. Derm faintly nodulose. Dorsal setae of two types: 1, minute subdigitate setae, 2–3 μm long, in a medial series on each side of abdominal segments II–VII; 2, enlarged setae, 5–17 μm long, with swollen bases and blunt to truncate apices, extending medial series with one seta on each side of abdominal

segment I, metathorax and mesothorax, two setae on each side of prothorax, and one seta on each side of head, one seta laterad of each medial seta on metathorax and mesothorax, plus one laterad of each anterior medial seta on prothorax, setation of abdominal segment I unstable, setae may be either subdigitate or enlarged. Margin with fringe of setae similar to enlarged dorsal setae, 6–13 μm long; one seta on each side of abdominal segments I–VII, two setae on each side of metathorax and mesothorax, four setae on each side of prothorax and 8–12 setae on head between eyes. Macrotubular ducts absent. Microtubular ducts in marginal series from head to abdominal segment VIII, plus one microtubular duct laterad of each medial seta on head and thorax. Disc pores absent.

Venter with flagellate setae 4–11 μm long, in four longitudinal rows on each side of abdomen, with marginal row extending through thorax and onto head; setae medial of coxae not detected, three pairs of setae on head, 12–20 μm long. Macrotubular ducts and microtubular ducts absent. Disc pores trilocular, 3 μm in diameter; in submedial series on either side

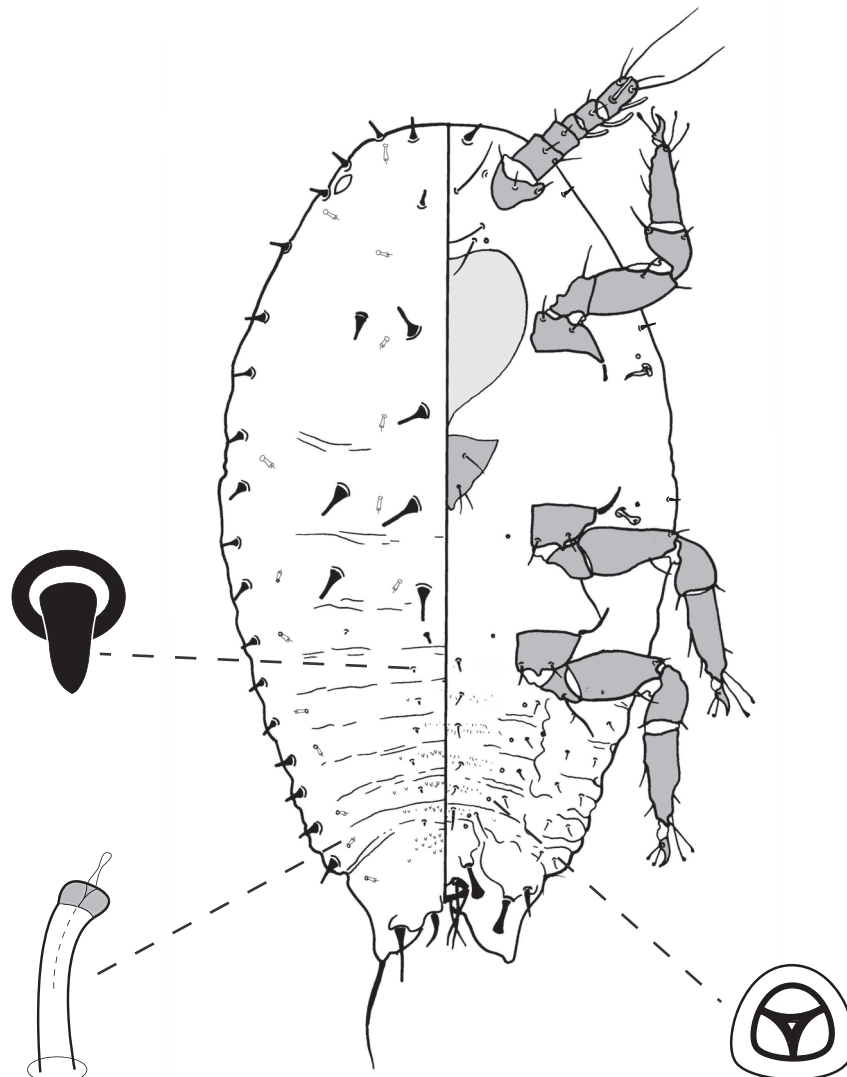


Fig. 8. First-instar nymph of *Madarococcus meander*, sp. nov.

of abdomen, one medial of each coxa, one on each side of head, laterad of elongate setae, and one near each spiracle.

Diagnostic features

The first-instar nymphs of *M. meander* can be distinguished from the other Australian species of *Madarococcus* by the presence of only one disc pore near each anterior spiracle and the absence of microtubular ducts on the dorsal submedial areas of the abdomen.

Etymology

This species name is derived from the Tasmanian locality where this species is common and which will be inundated by the controversial Meander Dam. The name is a noun in apposition.

*Madarococcus megaventr*s Hardy & Gullan, sp. nov.

(Figs 4G, 9)

Material examined

Holotype. New South Wales: 1 adult female: New England National Park, ex *N. moorei* in tubular leaf gall, 31.iii.1972, J. W. Beardsley (ANIC).

Paratypes. **New South Wales**: 5 adult females: same data as holotype (BPBM); 5 adult females: New England National Park, Styx River, Forest Way, c. 200 m NE of Beech Lookout, 30°30'58''S, 152°21'30''E, 1394 m, galls on leaves of *N. moorei*, 13.x.2006, M. D. Crisp & D. Morris (ANIC); 6 adult females: New England NP, Point Lookout, 30°28'32''S, 152°24'17''E, 1506 m, galls on leaves of *N. moorei*, 13.x.2006, M. D. Crisp & D. Morris.

Description

Adult female (Fig. 9)

Live material. The adult female of *M. megaventr*s induces finger-like galls (Fig. 4G) on the leaves of *N. moorei*. The dorsum is flat and plugs the gall opening and the venter is expanded to fill the gall cavity.

Mounted material. Body outline oblong, greatly expanded venter extending forward far beyond sclerotic dorsum, length 2.34–3.78 mm (holotype 2.74 mm), greatest width 0.76–1.16 mm (holotype 1.14 mm). Eyespot 14–16 µm wide, either incorporated into sclerotic dorsal derm, or just ventrad of it. Antennae 6-segmented; length 103–107 µm; with four hair-like setae (trichoid sensilla) on segment I, three hair-like setae on II, three hair-like setae on III, one fleshy seta on IV, four hair-like setae plus one fleshy seta on V, and c. seven hair-like setae plus three fleshy setae on VI. Frontal (interantennal) lobes not detected. Tentorial box 80–100 µm long, 57–80 µm wide. Labium 50–67 µm long, 50–57 µm wide; 3-segmented; seven pairs of setae on anterior surface, one pair of apical short setae, and one pair of setae on posterior surface. Spiracles 28–32 µm long, 15–17 µm wide across atrium. Legs subequal (except hind tarsus 7–10 µm longer than fore or mid tarsus); coxa 25–37 µm, trochanter + femur 75–95 µm, tibia 40–50 µm, tarsus 52–67 µm, claw 14–15 µm; fore coxa with five setae, mid and hind coxa each with six setae; trochanter with four setae (longest seta 27–39 µm), fore femora each with six setae, mid and hind femur each with five setae, fore tibia with five setae, mid tibia and hind tibia each with four setae, tarsus with four setae; tarsal digitules 20–26 µm, claw digitules dissimilar, 15–16 µm long, one with

apical knob 5 µm wide, other with apical knob 1 µm wide; c. five translucent pores on dorsal surface of hind coxa, not detected in some specimens. Anal ring 32–42 µm wide, invaginated, bearing six setae, 60–95 µm long. Suranal setae evenly attenuated, 30–45 µm long, each seta with origin adjacent to anal invagination. Anal lobes subconic, apex bicuspid – origin of ventral lobe seta more distal than that of caudal seta, ventral surface of lobes only weakly sclerotic; lobes each with c. three microtubular ducts; ventral lobe seta 33–44 µm long, dorso-lateral lobe seta 13–15 µm, dorsomedial lobe seta 15 µm and projecting mesad, often overlapping opposite lobe, dorsoapical lobe seta 18–20 µm, caudal seta 57–76 µm.

Dorsum. Derm largely sclerotic; lateral portions of abdominal segments II–VII occupied by subrectangular plates; submedial areas of each abdominal segment with smaller sclerotic fragments along anterior margin; most cuticle cephalad of abdominal segment II sclerotic. Dorsal setae spinose, 5–7 µm long; two pairs of medial setae on both head and prothorax, one pair of medial setae on other segments, abdominal segments may be missing one or both setae; one submedial seta on each side of head, two submedial seta on each side of prothorax, and one submedial seta on each side of mesothorax, metathorax and abdominal segment I; lateral area of abdominal segments with transverse series of three spinose setae, medial-most seta in line with a marginal row of setae extending around thorax and head, this row most distinct on head. Macrotubular ducts 6–10 µm long, with dermal orifice raised slightly above cuticle and vestibule sclerotic; in a transverse row across each posterior abdominal segment, rows becoming more staggered cephalad. Microtubular ducts ~5 µm long, with structure and distribution similar to macrotubular ducts. Where incorporated into sclerotic areas of dorsum, ducts originate from circular areas of membranous cuticle 3–9 µm in diameter.

Venter. Flagellate setae 5–18 µm long, in a transverse row across each of abdominal segments II–VII, three pairs of elongate (12–30 µm) setae on medial portion head. Tubular ducts absent. Quinquelocular pores 4 µm in diameter; clustered around spiracles, in broad submarginal band extending from bases of antennae to anal lobes. Abdominal segments II–VII not enlarged, size of venter owing to hyper-development of head, thorax and perhaps abdominal segment I.

Diagnostic features

It would be hard to confuse full-grown adult females of *M. megaventr*s with any other scale insect, due to the grossly distended venter. Adult females of *M. megaventr*s are most similar morphologically to those of *M. meander* and *M. cunicularius* [see comments under *M. meander*].

Remarks

Our analysis of the sequence data recovered strong support (PP = 1.0) for a sister-group relationship between *M. megaventr*s and *M. meander*, the only two species from Australia known to induce galls on *Nothofagus*.

Etymology

The species name is formed from the Latin terms *mega*, meaning large, and *ventris*, meaning belly, referring the spectacular distension of the ventral body surface of the adult female.

***Madarococcus montifagi* (Hoy), comb. nov.**

(Fig. 4H)

Eriococcus montifagi Hoy, 1962a: 108–109, fig. 40. Type data: **New Zealand**: South Island, Arthur's Pass, on *Nothofagus solandri* var. *cliffortioides*, 26.xii.1914, by G. Brittin. Holotype female, by original designation. Type depository: NZAC.

Acanthococcus montifagi; Miller & Gimpel, 1996: 602. Change of combination.

Material examined

New Zealand: TO, Ohakune Ranger Station, leaves of *N. solandri* (NZAC); MC, Lake Pearson, State Highway 73, forest by roadside, stem nodes or

curled on buds of *N. solandri* (ANIC, NZAC); MC, Craigieburn Forest Park, *N. solandri* underside leaves (NZAC).

Remarks

Hoy (1962a) mistakenly described dorsal macrotubular ducts on the adult female, but these occur along the ventral submargin in the holotype. Likewise, Hoy described the anal ring as having six setae, but eight are present. Hoy (1962a) did not record the location of the adult females on their host. Recent collections confirm that they do not form a test and are either 1, wrapped around buds at nodes, with the last few abdominal segments curled and the more anterior parts more convex and sclerotized,

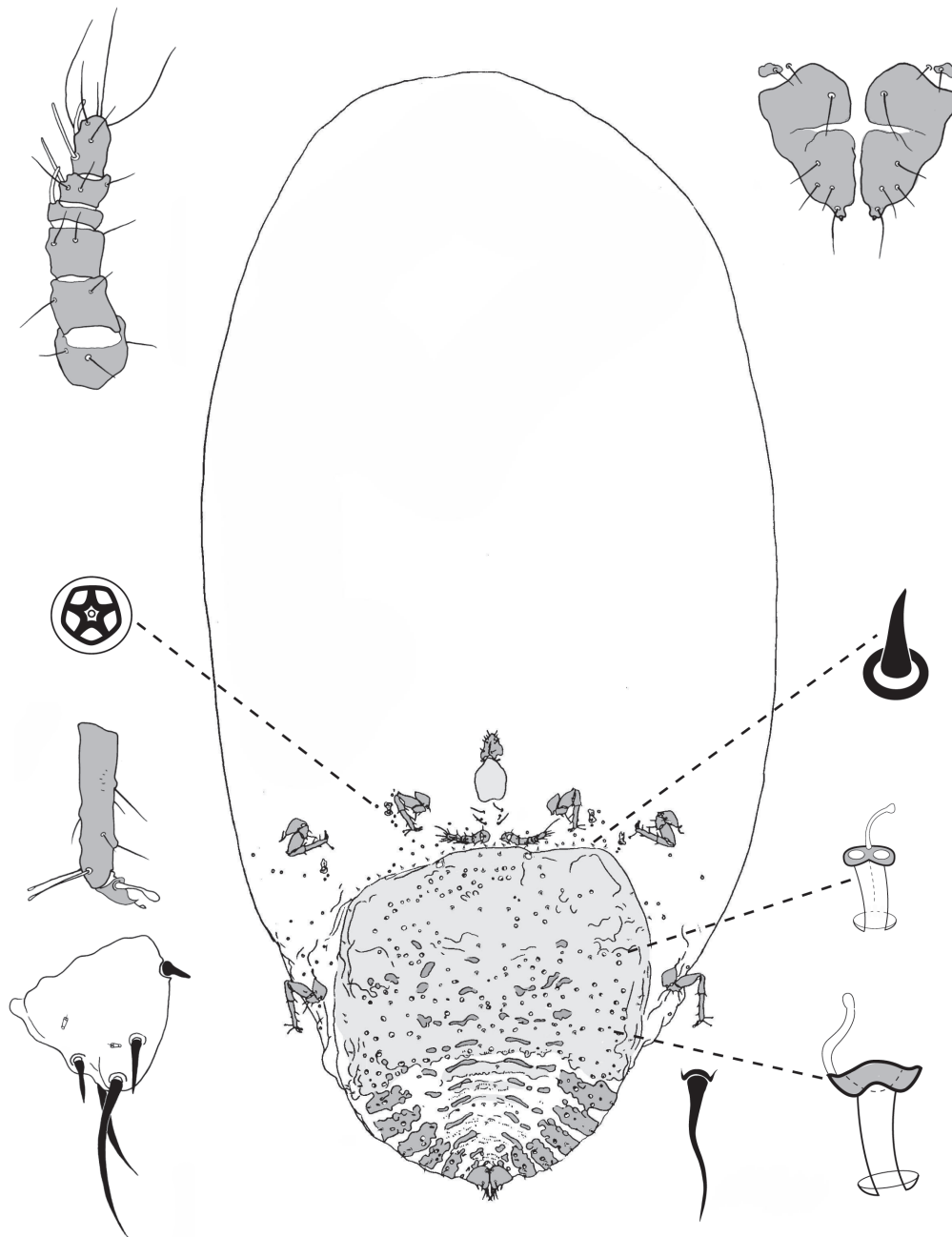


Fig. 9. Adult female of *Madarococcus megaventris*, sp. nov.

or 2, on the underside of leaves, becoming highly convex with a brood chamber beneath. *Madarococcus montifagi* is most similar to *M. detectus* [see comments under *M. detectus*].

***Madarococcus moorei* Hardy & Gullan, sp. nov.**

(Figs 4I, 10, 11)

Material examined

Holotype. New South Wales: 1 adult female: Barrington Tops State Forest, Dilgry Circle, 31°53'S, 151°32'E, ex foliage of *N. moorei*, 25.xi.1986, PJG and S. Bhatti (ANIC).

Paratypes. **New South Wales:** 13 adult females: same data as holotype (10 slides ANIC, one slide BMNH, two slides USNM); 19 adult females, 2 second-instar males, 14 second-instar females and c. 65 first-instar nymphs (seven slides with first- and second instar nymphs): Brooklana, off Old Coramba Rd, on Eve Creek, 30°17'S, 152°50'E, on foliage of *N. moorei*, 9.x.1996, PJG (ANIC); 11 adult females: New England NP, on *N. moorei*, 31.iii.1972, J. W. Beardsley (BPBM). **ACT:** 1 adult female: Canberra, Black Mt., Australian National Botanic Gardens, on underside of leaf of planted tree of *N. moorei*, 27.x.1996, PJG (ANIC).

Description

Adult female (Fig. 10)

Live material. Young females of this species feed in leaf axils and are highly cryptic. Adult females (Fig. 4I) occur primarily on the undersides of leaves and stems; body colour variable, from almost grey to dark brown, with a smooth dorsum and white wax fringe where body contacts host.

Mounted material. Body outline turbinate to circular, length 1.02–2.40 mm (holotype 1.98 mm), greatest width 0.62–2.00 mm (holotype 1.56 mm), dorsum larger than venter in more fully expanded specimens. Eyespot dorsad of margin, 32 µm wide. Antennae 7-segmented, segments III and IV incompletely fused; length 200–225 µm; with four hair-like setae (trichoid sensilla) on segment I, three hair-like setae on II, 0 setae on III, two hair-like setae on IV, one fleshy seta on segment V, 3–4 hair-like setae plus one fleshy seta on VI, and seven hair-like setae plus three fleshy setae on VII. Frontal (interantennal) lobes present, digitate. Tentorial box 125–150 µm long, 125–150 µm wide. Labium 85–100 µm long, 70–87 µm wide; 3-segmented; seven pairs of setae on anterior surface, one pair of setae on posterior surface, and one apical pair of short setae. Spiracles 45–50 µm long, 25–27 µm wide across atrium. Legs increasing in size caudad; fore legs: coxa 57–67 µm, trochanter + femur 157–185 µm, tibia 75–95 µm, tarsus 70–85 µm; mid legs: coxa 62–87 µm, trochanter + femur 172–197 µm, tibia 77–100 µm, tarsus 75–92 µm; hind legs: coxa 75–95 µm, trochanter + femur 180–215 µm, tibia 82–105 µm, tarsus 80–97 µm; claw 20 µm long; coxa with six setae, trochanter with four setae (longest seta 92–100 µm), fore femur with six setae, mid and hind femur each with five setae, tibia with four setae and tarsus with six setae; tarsal digitules 32–39 µm long; claw digitules similar, 22–25 µm long, apical knob 6 µm wide; translucent pores few, c. 15 in number, restricted to lateral surfaces of hind coxae and dorsodistal portions of hind femora. Anal ring 50–62 µm wide, bearing eight setae, 90–130 µm long. Suranal setae spatulate, 37–50 µm long. Anal lobes subconical, 90–110 µm long, apex bicuspid – origin of dorsoapical lobe seta

nearly as distal as origin of apical seta; one microtubular duct arising near base of each dorsal lobe seta, ~3 additional microtubular ducts in dorsal surface of each anal lobe; ventral lobe setae 25–36 µm, dorsolateral lobe seta 20–27 µm, dorsomedial lobe seta 14–20 µm, dorsoapical lobe seta 30–45 µm, caudal seta 107–117 µm.

Dorsum. Derm faintly nodulose. Dorsal setae of two distinct types: first type spinose, bases swollen, apices blunt to truncate, 25–32 µm long; second type curved, digitate, apices blunt, 7–10 µm long; setae of first type arranged in transverse rows, one row across each body segment except for prothorax with two transverse rows and abdominal segment VIII without setae, head with one transverse row of ~6 setae, plus one medial series on either side beginning just anterior of transverse row and wrapping around to ventral surface; smaller digitate setae restricted to submedial area of posterior abdominal segments; number of setae in each row increasing from tow on abdominal segment VII to ~14 on metathorax. Margin delineated by fringe of setae similar to those on dorsum, 17–30 µm long. Macrotubular ducts absent. Microtubular ducts 5–8 µm long, scattered over dorsum; 1–2 associated with bases of most spinose setae.

Venter. Flagellate setae mostly 7–25 µm long, in a transverse row across each abdominal segment; abdominal segments II–VII each with one pair of long (20–47 µm) submedial setae; longest setae medial of coxae 37–70 µm; setae on head posteromedial of antennal insertions 17–70 µm long. Macrotubular ducts 10–14 µm long, in broad marginal swath, a few medial of procoxae and mesocoxae. Microtubular ducts absent. Quinquelocular pores 4–5 µm in diameter, confined to areas of abdomen, metathorax and mesothorax mesad of macrotubular ducts.

Diagnostic features

Madarococcus moorei appears to be very closely related to *M. detectus*, in that both species lack macrotubular ducts on the dorsum, have a distinct marginal fringe of spinose setae, and numerous quinquelocular pores on the ventral medial areas of the abdominal segments. *Madarococcus moorei* can be distinguished from *M. detectus* by lacking a pit near the anterior margin of the dorsal surface of the anal lobes, and by lacking translucent pores on the hind tibiae.

Variation

Several specimens from Brooklana differ from the type material in having more of the curved digitate setae on the dorsum; in a few specimens these completely replace the spinose setae. In all other respects the Brooklana specimens match those from the type locality.

First-instar nymph (Fig. 11)

Mounted material. Body length 209–325 µm, greatest width 115–160 µm. Eyespot 10 µm wide, ventrad of margin. Antennae 6-segmented, 64–70 µm long; with four hair-like setae (trichoid sensilla) on segment I, two hair-like setae on II, two hair-like setae on III, one fleshy seta on IV, three hair-like setae plus one fleshy seta on V, and ~6 hair-like setae plus three fleshy setae on VI. Tentorial box 57–61 µm long, 42–48 µm wide. Labium 3-segmented, 27–34 µm long, 25–28 µm wide; seven

pairs of setae on anterior surface, one apical pair of short setae, and one pair of setae on posterior surface. Spiracles 11–15 μm long, 5 μm wide across atrium. Legs subequal; coxa 12–14 μm , trochanter + femur 47–50 μm , tibia 19–20 μm , tarsus 28–35 μm , claw 9–10 μm ; tarsal digitules 13–17 μm long, claw digitules 10–11 μm long, ventral digitule thicker than dorsal digitule. Anal ring 17–20 μm wide, bearing six setae, 30–34 μm in length. Suranal setae spatulate, 11–14 μm long. Anal lobes 25–30 μm long, with broad, truncate apex; ventral lobe seta 11–13 μm , dorsolateral lobe seta 9–10 μm , dorsomedial lobe

seta 10–12 μm , dorsoapical lobe seta 11–12 μm , apical seta 45–50 μm .

Dorsum. Derm nodulose. Dorsal setae 4–8 μm long, tapering to blunt apex, often curved; two medial series, with one seta on each side of head, two setae on each side of prothorax, and one seta on each side of mesothorax, metathorax and each of abdominal segments I–VII; one submedial series on each side of body extending from prothorax to abdominal segment I. Margin with distinct fringe of enlarged setae, 6–10 μm long, with swollen bases and blunt apices; one seta on each side of each

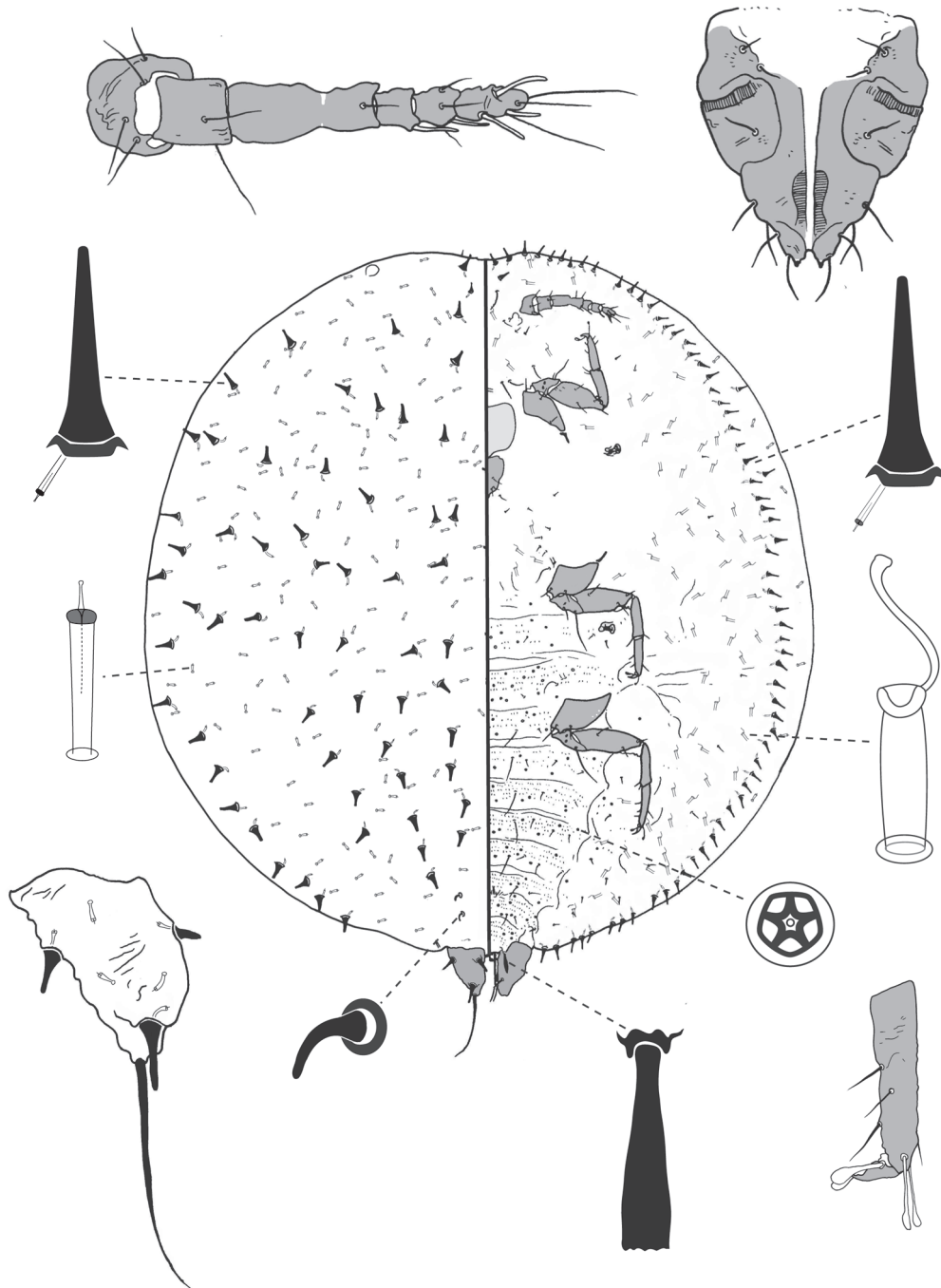


Fig. 10. Adult female of *Madarococcus moorei*, sp. nov.

abdominal segment, two on each side of metathorax and mesothorax, five on each side of prothorax, and five on each side of head. Macrotubular ducts absent. Microtubular ducts ~5 µm long; one anterior to each anal lobe, one laterad of medial setae on abdominal segments V and II, each thoracic segment, and one more in this submedial position just posterior of head, one mesad of marginal fringe setae on abdominal segments I and IV, plus one on each side of each thoracic segment and head.

Venter with setae 3–11 µm long, in four longitudinal rows on each side of abdomen – one marginal row on each side of body extending onto mesothorax, submarginal row on each side of body reaching metathorax, one medial and one submedial row on each side of body not extending beyond abdomen; setae medial of coxae 10–15 µm; three pairs of setae on head 10–15 µm long. Macrotubular ducts and microtubular ducts absent. Some disc pores quinquelocular, most trilocular, 3 µm in diameter; in one longitudinal series on either side of abdomen, laterad of medial setae, one medial of each coxa, one near each posterior spiracle, two near each anterior spiracle, and one on head lateral of elongate setae.

Diagnostic features

The first-instar nymphs of *M. moorei* can be distinguished from the other Australian species of *Madarococcus* by having digitate dorsal setae, all of which are much smaller than the marginal setae.

Etymology

This species is named for its host, *Nothofagus moorei*.

Madarococcus navarinoensis (Hoy)

Eriococcus navarinoensis Hoy, 1962b: 510–512, fig. 1. – Miller & González, 1975: 144–146, fig. 6. Type data: **Chile**: Navarino Island, Puerto Williams, on *N. betuloides*, 1958, E. Godley. Holotype and eight paratype females, by original designation. Type depository: NZAC.

Material examined

Chile: X Region, Parque Nacional Puyehue, Anticura, ex test on leaves of *N. nitida* (BME); IX Region, Parque Nacional Huerquehue, ex test on leaves

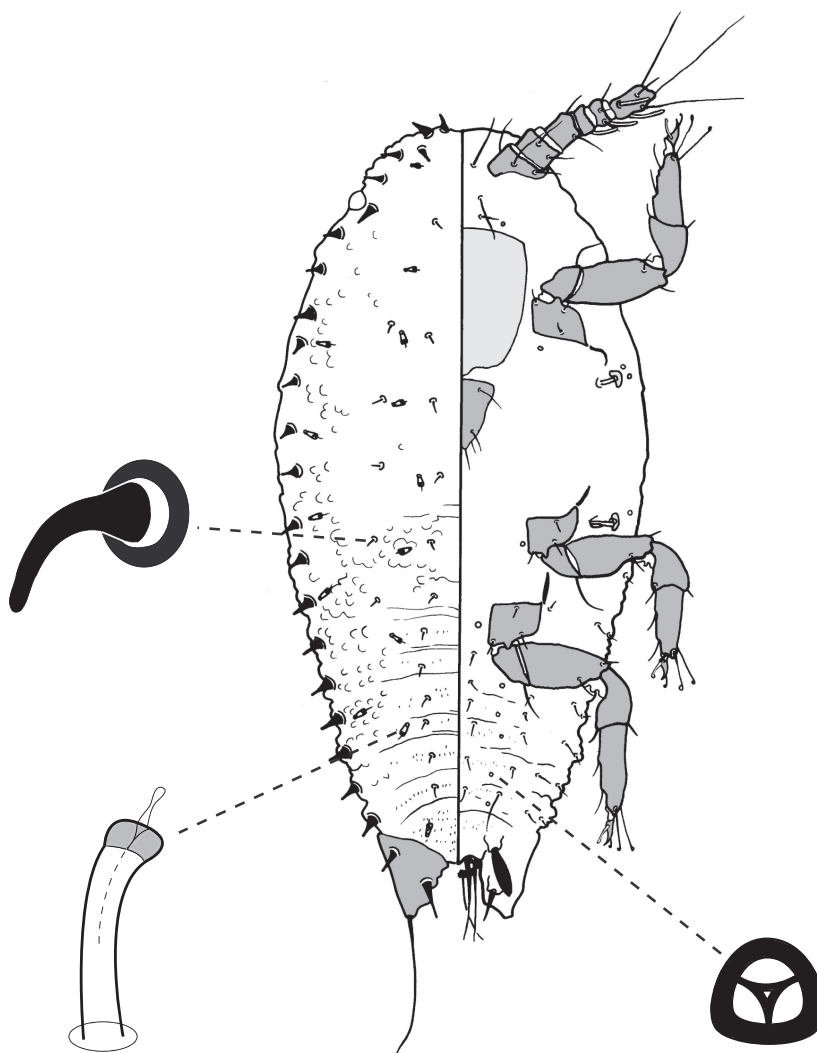


Fig. 11. First-instar nymph of *Madarococcus moorei*, sp. nov.

of *N. dombeyi* (ANIC, BME); X Region, near Rio Blanco, ex test on leaves of *N. nitida* (ANIC, BME) [see remark on these specimens below].

Remarks

The adult females of *M. navarinoensis* are very similar to those of *M. chilensis* [see comments under *M. chilensis*] and *M. rhadinothrix*. Miller and González (1975) separate the adult females of *M. navarinoensis* from those of *M. rhadinothrix* by 1, 19–31 dorsal setae on abdominal segment V on *M. navarinoensis* (9–14 on *M. rhadinothrix*); 2, setae on dorsomedial areas of head and thorax noticeably smaller than those on abdominal margin on *M. navarinoensis* (setae on dorsomedial areas of head and thorax *c.* same size as those along abdominal margin on *M. rhadinothrix*); 3, 7-segmented antennae on *M. navarinoensis* (6-segmented in *M. rhadinothrix*); 4, tibia:tarsus ratio 0.9–1.1 for *M. navarinoensis* (0.7–0.8 for *M. rhadinothrix*), and 5, anal lobes smaller, broader and less protuberant on *M. navarinoensis* than on *M. rhadinothrix*. They also suggest that the presence of translucent pores on the hind tibiae can be used to distinguish the adult females of *M. rhadinothrix* from those of *M. navarinoensis*, however, the figures show the reverse: translucent pores on the hind tibiae of *M. navarinoensis* and translucent pores absent from this location on *M. rhadinothrix*.

We have examined material from Rio Blanco in Chile and it is near to *M. navarinoensis* (with translucent pores on hind tibiae) except that only *c.* 14 setae are present on the dorsal surface of abdominal segment V, and the anal lobe is as long and protuberant as it is on *M. rhadinothrix*. In the phylogenetic analysis of the molecular data, we refer to the Rio Blanco material as *M. nr navarinoensis*. The type locality, Navarino Island, is located at latitude 55°S, but the species has been recorded from several more northerly localities at different altitudes in Chile and also occurs in Argentina. It is possible that some observed variation in setal and other features may be due to environmental effects, especially developmental temperature.

Madarococcus nelsonensis (Hoy), comb. nov.

(Fig. 4J)

Eriococcus nelsonensis Hoy, 1962a: 31, 114–115, fig. 43. Type data:

New Zealand: South Island, Takaka Hill, on *Nothofagus fusca*, 15.x.1935, G. Brittin. Holotype and eight paratype females, by original designation. Type depository: NZAC.

Acanthococcus nelsonensis; Miller & Gimpel, 1996: 602. Change of combination.

Material examined

New Zealand: BR, Springs Junction, Palmer Rd, leaf axils or stem of *N. fusca* (NZAC); MC, Banks Peninsula, Hinewai Reserve, *N. fusca* stems in leaf bud axils (Fig. FJ) (NZAC).

Remarks

In addition to the host record for the type material, Hoy (1962a) provides two other host records, *N. solandri* and *N. menziesii*, both of which were collections by G. Brittin. The enlarged hind coxae of *M. nelsonensis* might be confused with those of *M. cavellii*. Otherwise, the two species are easy to separate, *M. cavellii* having numerous spinose setae on the lateral areas of the venter, and *M. nelsonensis* having setae on the posterior abdominal segments much smaller than those found on the rest

of the dorsum. *Madarococcus nelsonensis* is most similar to *M. argentifagi*, *M. rubrifagi*, and *M. nothofagi* [see comments under *M. nothofagi*], but can be distinguished from these three species by the greatly enlarged hind coxae and numerous microtubular ducts on the ventromedial surface of the head.

Madarococcus nothofagi (Hoy), comb. nov.

Eriococcus nothofagi Hoy, 1962a: 31, 120–121, fig. 46. Type data: **New Zealand:** South Island, Owaka, on *Nothofagus menziesii*, 11.xi.1958, J. M. Hoy. Holotype and 23 paratype females, by original designation. Type depository: NZAC.

Acanthococcus nothofagi; Miller & Gimpel, 1996: 602. Change of combination.

Remarks

This species is similar to *M. argentifagi*, *M. rubrifagi*, and *M. nelsonensis*. Each of these species has the following combination of features: 1, pairs of minute setae on the posterior abdominal segments; 2, absence of a marginal fringe of enlarged setae but a characteristic arrangement of dorsal setae on the posterior abdominal segments: one enlarged seta on the margin of each abdominal segment plus one enlarged seta just medial of the margin, and 3, numerous macro-tubular ducts on the dorsum and ventral submargin. *Madarococcus nothofagi* can be easily distinguished from the other three species by the short apical lobe (caudal) setae, which are shorter than the dorsoapical lobe setae. This feature also is found in the Australian species *M. cunninghamii*.

Madarococcus occultus Hardy & Gullan, sp. nov.

(Fig. 12)

Material examined

Holotype. Tasmania: 1 adult female: 32 km [20 miles] W of Maydena, in ovisac under twig bract on *N. cunninghamii*, 26.vi.1972, J. W. Beardsley (ANIC).

Paratypes. **Tasmania:** 16 adult females (11 slides), eight of which are in poor condition, badly damaged by fungus, same data as holotype (BPBM).

Description

Adult female (Fig. 12)

Live material. The female of this species lives under the bracts of *N. cunninghamii* with its posterior margin protruding (McQuillan, 1993). The body of the adult female is orange-brown.

Mounted material. Body outline ovate to turbinate, length 1.12–1.44 mm (holotype 1.28 mm), greatest width 0.96–1.1 mm (holotype 0.98 mm). Eyespot just ventrad of margin, 15–20 µm wide. Antennae 6-segmented; length 120–137 µm; with four hair-like setae (trichoid sensilla) on segment I, three hair-like setae on segment II, 2–3 hair-like setae on segment III, one fleshy seta on segment IV, five hair-like setae and one fleshy seta on segment V, and *c.* six hair-like setae plus three fleshy setae on segment VI. Frontal (interantennal) lobes not detected. Tentorial box 105–112 µm long, 87–100 µm wide. Labium 55–70 µm long, 50–60 µm wide; 3-segmented, basal segment indicated

only by presence of basal segment setae; seven pairs of setae on anterior surface, one pair of setae on posterior surface, and one apical pair of short setae. Spiracles 35–48 μm long, 21–30 μm wide across atrium. Hind legs larger than fore or mid legs; fore and mid legs: coxa 30–42 μm , trochanter + femur 83–90 μm , tibia 37–44 μm , tarsus 45–55 μm ; hind legs: coxa 47–52 μm , trochanter + femur 100–110 μm , tibia 45–50 μm , tarsus 52–62 μm ; claw 15–18 μm long; coxa with six setae, trochanter with three setae, longest seta 45–50 μm long, fore femur with six setae, mid and hind femur each with five setae, tibia with four setae, and tarsus with six setae; tarsal digitules 24–29 μm

long; claw digitules asymmetrical, 15–20 μm long, one with apical knob 3 μm wide, other with apical knob 2 μm wide; translucent pores very large, 4–12 μm wide, dorsal surfaces of hind coxae, femora and tibiae appearing latticed, hind coxae each with *c.* 15 pores on ventral surface and *c.* 50 pores on dorsal surface, hind femora each with *c.* 50 pores on dorsal surface, and hind tibiae each with *c.* 10 pores on dorsal surface. Anal ring 30–34 μm wide, bearing six setae, 35–45 μm long. Suranal setae spatulate, 12–15 μm long. Anal lobes 45–52 μm long, with rounded tooth on medial margin distal of dorsoapical lobe seta, dorsal surface invested with two microtubular ducts;

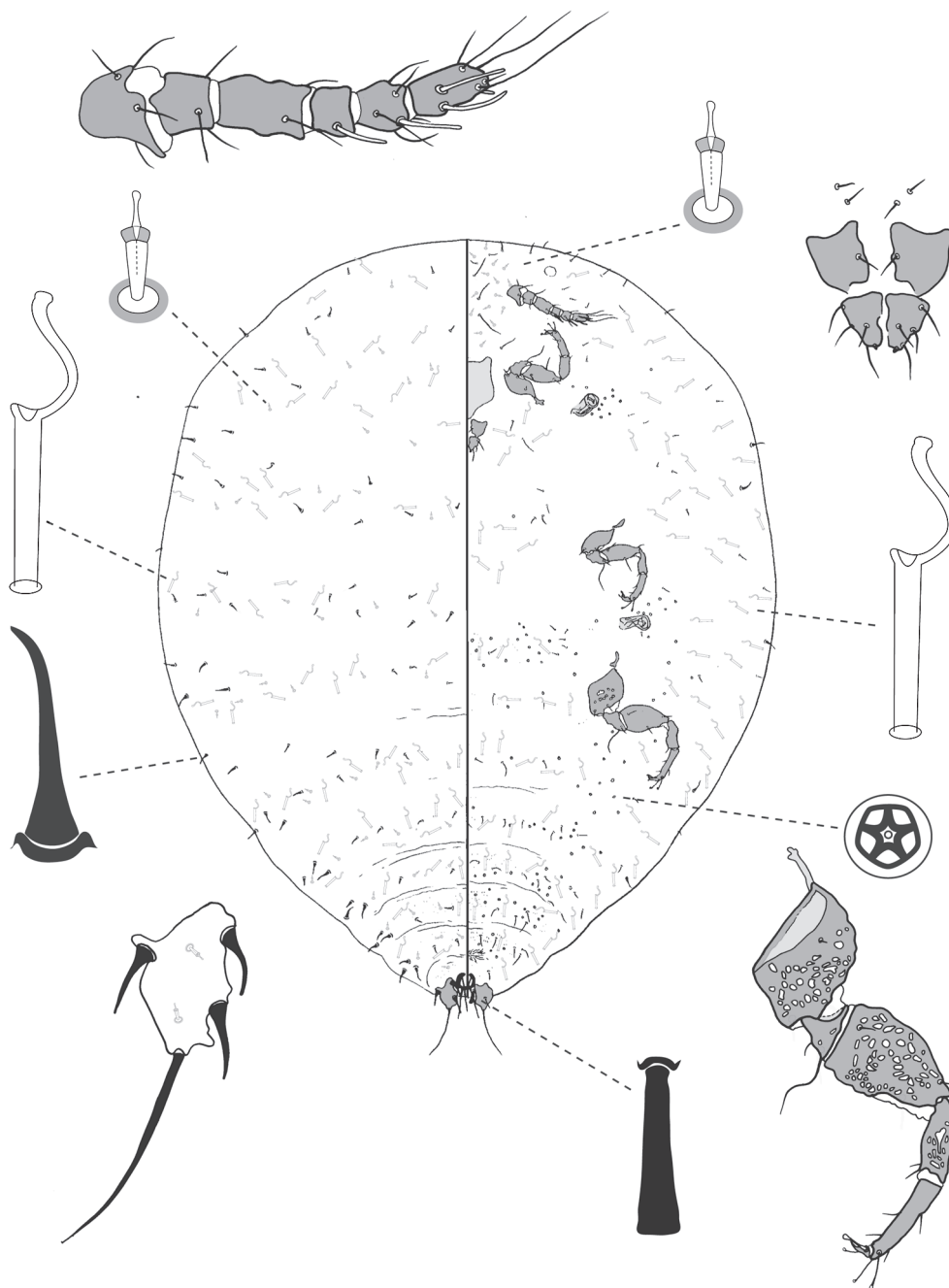


Fig. 12. Adult female of *Madarococcus occultus*, sp. nov.

ventral lobe seta 14–16 μm , dorsolateral lobe seta 27–32 μm , dorsomedial lobe seta 27–30 μm , dorsoapical lobe seta 27–32 μm , caudal seta 65–81 μm long.

Dorsum. Derm membranous. Dorsal setae 7–20 μm long, slender, slightly curved, with blunt apices; arranged in a transverse row across each body segment, rows becoming increasingly staggered cephalad; posterior abdominal segments each with a cluster of three enlarged setae (17–28 μm long) on each side near margin: two setae parallel to margin and one just ventrad of these, setae comprising marginal clusters becoming more widely dispersed cephalad. Macrotubular ducts 20–28 μm long, orifice *c.* 2 μm in diameter; densely distributed over dorsum. Microtubular ducts *c.* 5 μm long; found throughout dorsum, not associated with the bases of enlarged setae.

Venter. Flagellate setae 7–25 μm long, in a transverse row across medial portion of each abdominal segment plus some near margin, in clusters anteromedial of each mid and hind coxa, longest setae in these clusters 27–32 μm long, longest setae on head, medial of antennal insertions, 40–50 μm long. Macrotubular ducts like those on dorsum, found throughout venter. Microtubular ducts confined to a narrow medial band running between antennae from anterior margin of head. Quinquelocular pores 4 μm in diameter, in bands across abdominal segments, most dense around vulva and along a line running from anal lobes to hind coxae, in clusters around each spiracle, otherwise largely absent from head and thorax.

Diagnostic features

Surprisingly, *M. occultus* more closely resembles the Chilean species *M. eurythrix* than it does any of the Australasian species [see comments under *M. eurythrix*]. Nucleotide sequences of freshly collected specimens of *M. occultus* are needed to check its genetic affinities.

Etymology

This species takes its name from the Latin word meaning hidden or secret, referring to its cryptic habit under bracts of *N. cunninghamii*.

***Madarococcus osculus* Hardy & Gullan, sp. nov.**

(Fig. 13)

Material examined

Holotype. New South Wales: 1 adult female: New England National Park, ex underside of leaf of *N. moorei*, 31.iii.1972, J. W. Beardsley (ANIC).

Paratypes. **New South Wales:** 7 adult females, 1 pharate adult female partially enclosed in second-instar exuviae, and 1 adult male (6 slides); same data as holotype (BPBM).

Other material examined and excluded from type series. **Tasmania:** 1 adult female, Mt Field NP, Tarn Shelf, ex *N. gunnii* (TASAG); 1 adult female, Mt Field NP, Lyrebird Walk, ex *N. cunninghamii*, (TASAG); 1 adult female same data as previous except HeEr16 (TASAG).

Description

Adult female (Fig. 13)

Mounted material. Body outline elliptical, length 1.45–1.68 mm (holotype 1.64 mm), greatest width 0.86–1.02 mm (holotype 0.99 mm). Eyespot 24–30 μm wide, on

margin. Antennae 7-segmented, length 300–395 μm ; with three hair-like setae on segment I, one hair-like seta on II, 0 setae on III, two hair-like setae on IV, one fleshy seta on V, two hair-like setae plus one fleshy seta on VI, and seven hair-like setae plus three fleshy setae on VII. Frontal (interantennal) lobes present, digitate. Tentorial box 127–175 μm long, 135–153 μm wide. Labium 60–75 μm long, 87–112 μm wide; composed of two fused segments, basal segment lost; five pairs of seta on anterior surface, one apical pair of short setae, and one pair of setae on posterior surface. Spiracles 57–80 μm long, 29–40 μm wide across atrium, atria sclerotic. Legs increasing in size caudad; fore legs: coxa 67–82 μm , trochanter + femur 215–260 μm , tibia 110–132 μm , tarsus 100–107 μm ; mid legs: coxa 87–105 μm , trochanter + femur 237–295 μm , tibia 120–137 μm , tarsus 107–120 μm ; hind legs: coxa 100–132 μm , trochanter + femur 255–290 μm , tibia 125–137 μm , tarsus 112–125 μm ; claw 20–25 μm ; fore coxa with six setae, mid coxa and hind coxa each with five setae, trochanter with five setae (longest seta 72–125 μm), fore femur with five setae, mid and hind femur each with four setae (holotype has five setae on one hind femur), tibia with three setae, tarsus with five setae; tarsal digitules ~40 μm long; claw digitules dissimilar, 26–28 μm long, one with apical knob 10 μm wide, other with apical knob 4–6 μm wide; translucent pores on both surfaces of hind coxae, dorsal surface of each hind coxa with *c.* 30 pores concentrated laterally, ventrolateral surface of each hind coxa with *c.* 20 pores, medial region of ventral surface without pores, hind femora each with 15–20 translucent pores on dorsal surface. Anal ring 55–67 μm wide, bearing eight setae, 85–110 μm long. Suranal setae spatulate, 37–50 μm long. Anal lobes with oblique apex; dorsal surface of lobes invested with 7–9 microtubular ducts; ventral lobe seta 34–45 μm long, spinose or spatulate (perhaps always spatulate and only appearing spinose under certain orientations), arising on or near posterior margin, dorsolateral lobe seta 15–20 μm , dorsomedial lobe seta 10–15 μm , dorsoapical lobe seta 15–25 μm , caudal seta 70–86 μm .

Dorsum. Derm nodulose. Dorsal setae 8–11 μm long, spinose, with acute apices; in a transverse line across each posterior body segment, lines disintegrating cephalad, becoming random array. Margin delineated by fringe of enlarged setae, 21–31 μm long, with blunt apices; two setae on each side of each abdominal segment, three setae on each side of metathorax and mesothorax, five setae on each side of prothorax, and eight setae between eyes on head. Macrotubular ducts ~15 μm long, microtubular ducts ~5 μm long; both duct types densely distributed over dorsum, one microtubular duct associated with base of each marginal fringe seta.

Venter. Flagellate seta mostly 10–40 μm long, in an irregular disrupted transverse row across each abdominal segment; one submedial pair of long setae (42–70 μm) on abdominal segments II–VII; setae medial of coxae 60–75 μm ; setae on head postero-medial of antennal insertions 21–75 μm . Macrotubular ducts in marginal series, plus disjunct clusters in submarginal zones of abdominal segments. Microtubular ducts occurring amongst submarginal clusters of macrotubular ducts, plus a few in marginal zone of head and thorax. Quinquelocular pores 4–5 μm in diameter, in tight band extending from anal lobes to posterior spiracles, some incorporated into sclerotic peritremes of spiracles, pores radiating out from anterior spiracles to margin.

the type specimens of *M. osculus* in having far fewer macro-tubular ducts and setae on the dorsum (Tasmanian specimens with *c.* 20 macro-tubular ducts and four setae on abdominal segment VII; New South Wales specimens with *c.* 60 macro-tubular ducts and 16 setae on abdominal segment VII), and thus are excluded from the type series. The Tasmanian population may be a geographic variant of *M. osculus* or a new species. The specimens from *N. gunnii* are only eriococcids known from this *Nothofagus* species.

Etymology

This species name is taken from the Latin term *osculum*, meaning a small mouth, referring to the reduced labium.

Madarococcus papillosus (Hoy), comb. nov.

Sisyrococcus papillosus Hoy, 1962a: 181, 184–185, fig. 74. Type data: **New Zealand:** South Island, Motueka, Takaka Road [Takaka Hill for paratypes], on *Nothofagus fusca*, 8.ii.1920 [on *N. menziesii*, 15.x.1935 for paratypes], by G. Brittin. Holotype and six paratype females, by original designation. Type depository: NZAC.

Material examined

New Zealand: TO, Ohakune, Moore St, *N. menziesii*, (ANIC); NN, Kahurangi NP, Riwaka Resurgence, buds in leaf axils of *N. menziesii* (ANIC); NN, Takaka Hill Walkway, leaf buds in stem axils of *N. menziesii* (NZAC); DN, Dunedin Botanic Gardens, *N. menziesii*, stems in leaf bud axils (NZAC).

Remarks

Madarococcus papillosus is most similar to *M. intermedius* [see comments under *M. intermedius*]. In life, adult females of *M. papillosus* are pale green to pale or dark brown with a pale creamish dorsomedial longitudinal stripe and are covered with dorsal glassy wax tubes that each enclose a spiky seta. Small nymphs are pink to pale orange in life.

Madarococcus podocarpus (Hoy), comb. nov.

Eriococcus podocarpus Hoy, 1962a: 31, 134–135, 198, 206, fig. 53. Type data: **New Zealand:** South Island, Motueka, on *Dacrycarpus dacrydioides* (previously in *Podocarpus*), 17.xi.1918, by G. Brittin. Holotype female, by original designation. Type depository: NZAC. *Acanthococcus podocarpus*; Miller & Gimpel, 1996: 603. Change of combination.

Material examined

New Zealand: BR, St Arnaud, Lake Rotoiti (ANIC, NZAC).

Remarks

Madarococcus podocarpus was collected recently on *N. fusca*. The holotype specimen taken from *Dacrycarpus dacrydioides* represents the only collection of a *Madarococcus* species from a host other than *Nothofagus*. If the host was not misidentified, the most likely explanation for the original host record is either a labelling error or a chance occurrence on the wrong plant. It is impossible to identify *M. podocarpus* with the key of Hoy (1962a), as he relies incorrectly on the absence of translucent pores from the hind coxae. *Madarococcus podocarpus* is quite similar to *M. maskelli* [see comments under *M. maskelli*].

Madarococcus pulchellus (Maskell)

Rhizococcus pulchellus Maskell, 1891: 143–144, pl. VII, Figs 1–5.

Type data: **New Zealand:** Rimutaka Hills near Wellington, Caplestone, Reefton, Picton, on *Nothofagus solandri* (as *Fagus*), viii.1889, W. M. Maskell. Lectotype female (here designated; see below for details and discussion) and four paralectotype females (see below). Type depositories: NZAC and USNM.

Nidularia pulchellus; Lindinger, 1933: 116. Change of combination.

Madarococcus pulchellus; Hoy, 1962a: 6, 151, 158–159, fig. 64. Change of combination.

Material examined

New Zealand: NC, *c.* 12 km S of Lewis Pass, leaf undersides of *N. solandri* var. *cliffortioides* (ANIC); MC, Klondyke Corner, leaf undersides of *N. solandri* var. *cliffortioides* (ANIC).

Remarks

Hoy (1962a) illustrated and redescribed the adult female of this species. Although Maskell (1891) reported this species from three *Nothofagus* species, the only slide-mounted material was collected from *N. solandri*. Thus Hoy (1962a) recognised only specimens from this host as *M. pulchellus*. Thus we have designated a lectotype for this species in order to fix and stabilise Maskell's concept of the name. The lectotype slide of this species is labelled: 'Rhizococcus pulchellus / female 2nd-stage / on Fagus solandri / Aug. 1889 W.M.M.' but the specimen is a young adult female (1.6 mm long and 0.93 mm wide). Another slide-mounted Maskell specimen has the same label except 'female - adult' however it is an uncleared female with waxy filaments and cuticular details are obscured. Thus it was not selected as the lectotype, but we have labelled it as a paralectotype. Both of these original Maskell slide-mounts are in the NZAC together with a Hoy slide-mount labelled 'PLESIOTYPE' (remounted by RCH) of an adult female of this species from Maskell Collection 103 collected on *N. solandri* in August 1889. We also consider this latter female to be a paralectotype. The USNM has one slide-mount of an adult female from Maskell collection No 103, and thus we also recognise this specimen as a paralectotype. In addition the USNM as one box of dry material apparently from Maskell that was acquired as part of the Cockerell Collection and labelled as from New Zealand on 'Fagus' (D. R. Miller personal communication), but we are uncertain of the type status of this material.

Madarococcus pulchellus is closely related to *M. viridulus*, but the two species occur on different hosts (*N. solandri* and *N. fusca*, respectively). Both species are characterised by 1, rugose anal lobes, each with a large and conspicuous pit in the dorsal surface near the anterior margin; 2, a complete absence of macro-tubular ducts; 3, dorsal body surface densely beset with enlarged setae that in life secrete a glassy wax that forms a tube around the seta and projects from the body, and 4, in life, a light green body colour with patterned areas of white cuticle on the dorsum. *Madarococcus pulchellus* is distinguished by having the size of the dorsal setae vary continuously, in contrast to the dorsal setae in *M. viridulus* that cluster into two discrete size classes.

Madarococcus raithbyi (Maskell), comb. nov.

Eriococcus raithbyi Maskell, 1890: 145–146, pl. IX, figs 1–18. – Hoy, 1962a: 138–139, fig. 55. Type data: **New Zealand**: on *Nothofagus menziesii* (as *Fagus menziesii*). Lectotype female, by subsequent designation of Deitz & Tocker, 1980: 48. Type depositories: NZAC, BNHM, USNM.

Nidularia raithbyi; Lindinger, 1933: 116. Change of combination.

Acanthococcus raithbyi; Miller & Gimpel, 1996: 603. Change of combination.

Remarks

Hoy (1962a) illustrated and redescribed the adult female of this species based on one slide-mounted female from Maskell (this specimen is now the lectotype) plus eight additional specimens from Maskell's duplicate material, one of which he designated as a plesiotype. The lectotype slide is a Maskell original slide, labelled Holotype by Brittin then lectotype by Deitz & Tocker. Hoy's 'plesiotype' is labelled 'Eriococcus raithbyi/ Maskell Collection/ X *Nothofagus menziesii*/ 1889' and 'Stained & remounted by RC Henderson July 2006.' Hoy (1962a) described quinquelocular pores on the dorsum, however these pores occur only on the ventral body surface. Hoy also failed to note the presence of relatively enlarged setae on the margin, forming a loose fringe. There is some probable paralectotype material in the USNM but the status of Maskell material sent to the USA is uncertain. The USNM has two slides (one with an adult female containing several embryos and the other with several first-instar nymphs) labelled as Maskell No. 115, as well as two boxes of dry material (one has Maskell No. 54 and the other is a large circular box labelled from New Zealand on *Fagus* in Maskell's handwriting) (D. R. Miller personal communication). There is no Maskell material in the NZAC with the numbers 54 or 115. There are also two slides in the BMNH that may be paralectotype material. One slide has an adult female with the data: 'Eriococcus raithbyi Mask. ex-coll. Maskell', and on the envelope are the additional data 'on *Fagus menziesii*, New Zealand, BM 1940-180'. The other slide has two specimens, possibly nymphs (stylets in a loop), in badly deteriorated mountant, with the legend 'Eriococcus raithbyi Maskell, New Zealand, ex-coll. Maskell, July 1890, BM 1945-121' The second label simply has 'R Newstead' (J. H. Martin personal communication).

Madarococcus rhadinotrix (Miller & González)

Eriococcus chilensis Miller & González, 1975: 146–147, fig. 7. Type data: **Chile**: near Pucón, ex *N. obliqua*, 18.xii.1971, R. González. Holotype and four paratype females, by original designation. Type depositories: UCH; BMNH; BME; USNM.

Material examined

Argentina: c. 60 km NW of Bariloche, near Chilean border, on leaves of *N. dombeyi* (ANIC). **Chile**: Parque Nacional Alerce Andino, on leaves of *N. nitida* (ANIC).

Remarks

Adult females of *M. rhadinotrix* are very similar to those of the Chilean species *M. chilensis* and *M. navarinoensis* [see comments under *M. chilensis* and *M. navarinoensis*]. In the original description (Miller and González 1975), the field features of this species were recorded as unknown. The adult females listed

above as additional material had creamy orange tests and the specimens from Chile had eggs under their tests; tests mostly occurred on the underside of leaves but occasionally in twig axils.

Madarococcus rotundus (Hoy), comb. nov.

(Fig. 4K)

Eriococcus rotundus Hoy, 1962a: 142, fig. 57. Type data: **New Zealand**: South Island, Nelson, Stanley Brook, on *Nothofagus solandri* var. *solandri*, 04.iii.1960, J. M. Hoy. Holotype and 13 paratype females by original designation. Type depository: NZAC.

Acanthococcus rotundus; Miller & Gimpel, 1996: 603. Change of combination.

Material examined

New Zealand: AK, Hunua Range, Mangatangi Trig Track, *N. truncata* (NZAC); NN, Harwoods Hole, *N. solandri* underside leaves and on leaf buds (NZAC); BR, Inangahua, Fletchers Creek, *N. fusca*, (NZAC); BR, Reefton Saddle, Slab Hut Creek, *N. fusca* (NZAC); MC, Banks Peninsula, Hinewai Reserve, *N. fusca*, distorted curled shoots and underside of leaves near margin 21.viii.2001, on new leaf shoots 1.xi. 2001, leaves near margin 22.i.2002, on distorted curled shoots 4.vi.2002 (NZAC).

Remarks

Adult females of *M. rotundus* frequently occur on the underside of leaves and have a distinctive test pattern composed of curled wax strands (Fig. 4K). This species is very similar to *M. latilobatus* [see comments under *M. latilobatus*].

Madarococcus rubrifagi (Hoy), comb. nov.

Eriococcus rubrifagi Hoy, 1962a: 144, fig. 58. Type data: **New Zealand**: North Island, Rangataua, on *Nothofagus fusca*, 23.iii.1960, J. M. Hoy. Holotype and one paratype female, by original designation. Type depository: NZAC.

Acanthococcus rubrifagi; Miller & Gimpel, 1996: 603. Change of combination.

Material examined

New Zealand: BR Reefton Saddle, Slab Hut Creek, *N. fusca* (NZAC).

Remarks

Madarococcus rubrifagi is very similar to *M. argentifagi* [see comments under *M. argentifagi*]. It is also similar to *M. nelsonensis* and *M. nothofagi* [see comments under *M. nothofagi*]. The adult females of *M. rubrifagi* differ from those of *M. nelsonensis* by having the hind legs approximately as large as the fore and mid legs (hind legs much larger than fore and mid legs in *M. nelsonensis*). The adult female of *M. rubrifagi* can be distinguished from those of *M. nothofagi* by having caudal setae longer than the dorsoapical lobe setae (the opposite is true in *M. nothofagi*) and 7-segmented antennae (6-segmented in *M. nothofagi*).

Madarococcus viridulus Hoy

(Fig. 4L)

Madarococcus viridulus Hoy, 1962a: 162–163, fig. 66. Type data: **New Zealand**: North Island, Ohakune, on *Nothofagus fusca*, 10.ii.60, J. M. Hoy. Holotype and 28 paratype females, by original designation. Type depository: NZAC.

Material examined

New Zealand: BP, Rereauira Swamp, *N. truncata* (NZAC); NN, Flora Saddle, *N. fusca* underside leaves (NZAC); NN, Golden Bay, undersides of leaves of *N. truncata* (NZAC); NN, Whangamoia Saddle, Slaters Rd, underside of leaves of *N. truncata* (NZAC); NN/BR, above Buller River, c. 7 km E of Lyell, undersides of leaves of *N. fusca* (ANIC); BR, Rahu Saddle, Klondyke Spur Tk, leaf of *N. fusca* (NZAC); BR, Lewis Pass National Park, Marble Hill, *N. fusca* in dimples on underside of leaves (NZAC); MC, Banks Peninsula, Hinewai Reserve, *N. fusca* in dimples on underside of leaves (NZAC).

Remarks

Hoy (1962a) inspected Maskell's duplicate material labelled as *Rhizococcus pulchellus*. All material collected from *N. solandri* he recognised as *M. pulchellus* [see explanation in notes for that species]. The material collected from *N. fusca* he described as a new species, *M. viridulus*. The two species are very similar [see comments under *M. pulchellus*] and both live on the leaves of their hosts (Fig. 4L). However, females of *M. viridulus* induce dimples on leaves, as described and illustrated by Henderson and Martin (2006), whereas females of *M. pulchellus* do not distort the foliage. The NZAC has several collections of specimens that are similar to *M. viridulus* except that the dorsal body setae of the adult female are mostly minute, with two longitudinal medial rows of enlarged medial setae extending from the head to the tip of the abdomen and three pairs of submedial enlarged setae on the thorax. These specimens are all from *N. truncata* in the East Cape (North Island) and Nelson (South Island) regions (see above for collection data), and there is a range of variation in size of the enlarged setae, with most specimens from the Nelson region being closer to *M. viridulus* than those from the East Cape. These differences may represent variation within *M. viridulus*, perhaps due to host-plant differences.

Species excluded from *Madarococcus*

'*Madarococcus totarae*' (Maskell) *incertae sedis*

Rhizococcus totarae Maskell, 1890: 142–143, fig. 65. Type data: **New Zealand:** South Island, near Reefton, on *Podocarpus totara*, viii.1889, W. M. Maskell. Lectotype female, by subsequent designation of Deitz & Tocker, 1980: 49. Type depository: NZAC, USNM.

Nidularia totarae; Lindinger, 1933: 117. Change of combination.

Madarococcus totarae; Hoy, 1962a: 6, 151, 160–161. Change of combination.

Material examined

Material of typical form (some listed in Hoy (1962a) and some additional): **New Zealand:** AK, Waitakere Ra, Karamatura Stm, young stems of *Podocarpus totara* (NZAC); GB, Gisborne, on *P. totara*, (NZAC); TO, Ohakune, on *P. totara* (NZAC); NN, Nelson, on *P. totara* (NZAC); NN, Brightwater, ex *P. totara* (NZAC); NN, Motueka (NZAC); MC, Christchurch, Kennedy's Bush, on *P. totara* (NZAC).

Material of '*M. nr totarae*' (some listed in Hoy (1962a) and some additional): **New Zealand:** AK, Riverhead Forest, Barlow Road Reserve, stems of *P. totara* (ANIC); TO, Murupara, on *P. totara* (NZAC); TO, Pureora Forest (NZAC); WN, Otaki Forks, on *P. totara* (NZAC); MC, Akaroa, Grehan Valley, on *P. totara* (NZAC).

Remarks

Hoy (1962a) illustrated and redescribed the adult female of this species based on one slide-mounted female from Maskell's col-

lection (this female is now the lectotype) plus 44 other specimens collected subsequent to the original description. Maskell (1890) recorded this species from *Podocarpus totara* and sometimes on *N. menziesii*. Hoy noted that there were no specimens of this species from *Nothofagus* in Maskell's collection and that all subsequent records have been from podocarps. Thus it seems that Maskell's record from *Nothofagus* is erroneous. The entry for this species in ScaleNet (Miller and Gimpel 2007) and the recent world catalogue of Eriococcidae (Miller and Gimpel 2000) refers to paralectotypes in the USNM. The USNM has two slides (one with an adult female containing several embryos and the other with a piece of a pupa) (D. R. Miller personal communication). These have the Maskell Collection # 108. There are no specimens with the number 108 in the Maskell collection in the NZAC and the type status of the USNM material is uncertain.

Examination of all NZAC specimens studied by Hoy as well as subsequent collections revealed adult females and first-instar nymphs of two morphological forms collected from *P. totara* throughout New Zealand. In the typical form (i.e. the same as the lectotype), the adult female and associated first-instar nymph have conical enlarged marginal setae but only minute dorsal setae (with the exception of on embryo among several on the slide from Kennedy's Bush, which has two dorsal medio-longitudinal rows of small conical setae). In contrast, on specimens referred to here as '*M. nr totarae*', there are conical enlarged setae, 10–15 µm long (similar to those on the margin), on the mediadorsal thorax and anterior abdomen of the adult female, and on the first-instar nymph, there are two medio-longitudinal rows of conical setae, with each seta slightly wider at the base than the marginal conical setae. The distributions of these two morphological forms display no obvious altitudinal or latitudinal pattern and it is possible that we are dealing with two distinct but very closely related species. The collection used for DNA sequencing belongs to '*M. nr totarae*', but we are confident that both the typical form and '*M. nr totarae*' belong in the same clade based on their morphological similarity.

Phylogenetic analyses based on both morphological and molecular data place '*M. nr totarae*' well outside of the *Nothofagus*-feeding clade of eriococcids. The suranal setae of adult females of '*M. nr totarae*' and '*M. nr totarae*' are not spatulate (mostly spatulate in *Madarococcus*), and only one size class of quinquelocular pores is present on the venter (two size classes present in all but one of the *Madarococcus* species lacking spatulate suranal setae). We here transfer '*M. nr totarae*' out of *Madarococcus* and leave it unplaced (as *incertae sedis*) until its relationships can be better studied. It appears to be related to some other New Zealand species that feed on Podocarpaceae and currently are placed in *Eriococcus*. However the type species of *Eriococcus*, *E. buxi* (Boyer de Fonscolombe), is unrelated to the New Zealand *Eriococcus* species [see Cook *et al.* (2002) and Cook and Gullan (2004) for more information].

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Appendix 1. Collection data, museum depositories and GenBank accession numbers for specimens of species included in the molecular and morphological phylogenetic analyses

The specimen codes allow nucleotide sequences to be matched to slide-mounted voucher specimens in the depositories (see 'Materials and Methods' for names of depositories). In the 'Host' column, the first cell for each *Madarococcus* species lists all known host species; full host ranges are not given for outgroups. The 'Morphology' column specifies which specimens were used for the phylogenetic analysis of morphological data; c, crawler; e, embryo; f, adult female. Abbreviations: Ck, Creek; NP, National Park; PN, Parque Nacional; Ra, Range; RN, Reserva Nacional; SF, State Forest

Species [new names in bold]	Code	Hosts	Collection locality (*indicates not part of natural range)	Morphology	Depository	18S	EF-1 α	28S	wg
MADAROCOCCUS									
<i>Madarococcus argentifugi</i> (Hoy)		<i>Nothofagus menziesii</i> <i>N. menziesii</i>	New Zealand SL, Purakaunui Falls	2 paratype f	NZAC				
<i>M. cavellii</i> (Maskell)		<i>N. fusca</i> , <i>N. menziesii</i> , <i>N. solandri</i>	New Zealand						
	04-047c, 04-060a	<i>N. solandri</i> unknown	MC, Christchurch Maskell Coll., no locality	1 f, 8 c 1 f	NZAC NZAC				
	LGC361 02-177a,g	<i>N. solandri</i> <i>N. fusca</i>	NC, Klondyke Corner MC, Banks Peninsula	4 f	NZAC	EU746818		EU746858	
<i>M. chilensis</i> (Miller & González)		<i>N. betuloides</i> , <i>N. pumilio</i> <i>N. betuloides</i>	Chile Magallanes, Puerto del Hambre	2 paratype f	USNM				
		<i>N. pumilio</i> <i>N. fusca</i> , <i>N. sp.</i>	Parque Nacional Puyehue New Zealand	7 f	ANIC, BME				
<i>M. cruriamplius</i> Hoy		<i>N. sp.</i>	BR, Maruia Springs	3 paratype f	NZAC				
<i>M. cunicularius</i> Hoy	LGC163	<i>N. fusca</i> , <i>N. menziesii</i> <i>N. menziesii</i>	New Zealand BR, Mt Robert, 900 m	4 f	ANIC	EU746821	EU746873	EU746861	
<i>M. cunninghamii</i> , sp. nov.		<i>N. cunninghamii</i>	Australia						
	Madecun1	<i>N. cunninghamii</i>	Tasmania, Ridgley	composite of types	ANIC, TASAG	EU746819	EU746874	EU746859	EU746925
	LGC576	<i>N. cunninghamii</i>	Tas., c. 2 km N Columba Falls		ANIC	EU746820	EU746875	EU746860	EU746929
<i>M. detectus</i> (Hoy)		<i>N. solandri</i>	New Zealand						
<i>M. erythrix</i> (Miller & González)		<i>N. solandri</i> <i>N. alpina</i> , <i>N. antarctica</i> , <i>N. obliqua</i>	MC, Christchurch Chile	1 paratype f	NZAC				
	LGC319	<i>N. alpina</i>	Villarrica	3 f (voucher lost)	ANIC, BME	EU746814	EU746876	EU746852	EU746916
	LGC320	<i>N. obliqua</i>	Villarrica	1 f, 10 c	ANIC	EU746815	EU746877	EU746853	EU746917
	LGC581	<i>N. obliqua</i>	X Region, Hotel Peulla nr Villa Portales	4 f (1 for DNA)	BME	EU746816	EU746878	EU746854	EU746918
<i>M. fagicorticis</i> (Maskell)		<i>N. antarctica</i> <i>N. obliqua</i> <i>N. fusca</i>	Cautín, Pucón New Zealand	1 paratype f 1 paratype f	BME BME				
		<i>N. sp.</i> <i>N. fusca</i>	NN, Nelson, Lake Sylvester WN, York Bay	3 f 1 f, embryos	NZAC NZAC				
<i>M. hispidus</i> (Hoy)		<i>N. solandri</i> , <i>N. truncata</i>	New Zealand						
	93-298	<i>N. truncata</i>	GB, Kakamui	3 f	NZAC				
	93-289	<i>N. solandri</i>	BP, Te Koa	2 f, 4 c	NZAC				
<i>M. intermedius</i> (Maskell)		<i>N. menziesii</i>	New Zealand						
	LGC158	<i>N. menziesii</i>	WD, Haast Valley, Pleasant Flat	3 f	ANIC	EU746827	EU746880	EU746867	
	NZ2	<i>N. menziesii</i>	TO, Ohakune, Moore St	4 f, c.25 c	ANIC	EU746826	EU746881	EU746869	
	LGC164	<i>N. menziesii</i>	BR, Mai Mai Valley Rd		ANIC	EU746828	EU746879	EU746868	

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Appendix 1. (continued)

Species [new names in bold]	Code	Hosts	Collection locality (*indicates not part of natural range)	Morphology	Depository	18S	EF-1 α	28S	wg
<i>M. latilobatus</i> (Hoy)	58/44	<i>N. solandri</i> <i>N. solandri</i> <i>N. solandri</i> <i>N. fusca</i> , <i>N. solandri</i> , <i>N. truncata</i> <i>N. solandri</i> <i>N. fusca</i> <i>N. menziesii</i> , <i>N. solandri</i>	New Zealand OL, Lake Wakatipu, Lumberbox Ck OL, Lake Wakatipu, Lumberbox Ck New Zealand	5 paratype f 1 paratype f	NZAC NZAC				
<i>M. maculatus</i> (Maskell)		<i>N. solandri</i> <i>N. fusca</i> <i>N. menziesii</i> , <i>N. solandri</i>	Maskell Coll., Reefton TO, Okahune New Zealand	1 f 1 f	NZAC NZAC				
<i>M. maskelli</i> (Hoy)		<i>N. solandri</i> <i>N. solandri</i> <i>N. cumminghamii</i> <i>N. cumminghamii</i> <i>N. moorei</i> <i>N. moorei</i>	MC, Lake Pearson, State Hwy 73 Australia Tasmania, Meander SF Tasmania, Meander SF Australia NSW, New England NP	2 f composite of types 1 f composite of types	NZAC ANIC, TASAG ANIC BPBM, ANIC	EU746823 EU746822	EU746863	EU746865, EU746927, EU746864 EU746928	
<i>M. meander</i> , sp. nov.	05-167a	<i>N. solandri</i> <i>N. cumminghamii</i> <i>N. cumminghamii</i> <i>N. moorei</i> <i>N. moorei</i>	MC, Lake Pearson, State Hwy 73 Australia Tasmania, Meander SF Tasmania, Meander SF Australia NSW, New England NP	2 f composite of types 1 f composite of types	NZAC ANIC, TASAG ANIC BPBM, ANIC	EU746823 EU746822	EU746863	EU746865, EU746927, EU746864 EU746928	
<i>M. montifagi</i> (Hoy)	02-304b LGC370	<i>N. solandri</i> <i>N. solandri</i> <i>N. solandri</i> <i>N. moorei</i> <i>N. moorei</i>	New Zealand MC, Craigieburn Forest Park MC, Lake Pearson, State Hwy 73 Australia ACT, Canberra, Aust. Nat . Bot. Gardens	1 f 1 f 1 f composite of types	NZAC ANIC ANIC ANIC	EU746824		EU746866 EU746929	
<i>M. moorei</i> , sp. nov.	madar5	<i>N. moorei</i> <i>N. moorei</i>	ACT, Canberra, Aust. Nat . Bot. Gardens	1 f composite of types	ANIC ANIC	EU746824		EU746866 EU746929	
<i>M. navarinoensis</i> (Miller & González)		<i>N. moorei</i> <i>N. betulooides</i> , <i>N. dombeyi</i> <i>N. dombeyi</i> <i>N. nitida</i> <i>N. nitida</i> <i>N. fusca</i> , <i>N. menziesii</i> , <i>N. solandri</i> <i>N. fusca</i>	NSW, Barrington Tops SF Chile Parque Nacional Huerquehue Chile Rio Blanco New Zealand MC, Banks Peninsula, Hinewai Res. New Zealand SL, Owaka Australia Tasmania, Maydena Australia NSW, New England NP New Zealand TO, Ohakune, Moore St NN, Kahurangi NP New Zealand BR, St Arnaud, Lake Rotoiti	composite of types 3 f (1 for DNA) 4 f (1 for DNA) 4 f, 2 pharate f, 12 c 10 paratype f, mature e composite of types composite of types	ANIC ANIC ANIC, BME ANIC, BME ANIC, BME NZA NZAC BPBM, ANIC BPBM, ANIC	EU746817	EU746849 EU746919		
<i>M. nr navarinoensis</i>	LGC577	<i>N. dombeyi</i> <i>N. nitida</i> <i>N. nitida</i> <i>N. fusca</i> , <i>N. menziesii</i> , <i>N. solandri</i> <i>N. fusca</i>	Parque Nacional Huerquehue Chile Rio Blanco New Zealand MC, Banks Peninsula, Hinewai Res. New Zealand SL, Owaka Australia Tasmania, Maydena Australia NSW, New England NP New Zealand TO, Ohakune, Moore St NN, Kahurangi NP New Zealand BR, St Arnaud, Lake Rotoiti	3 f (1 for DNA) 4 f (1 for DNA) 4 f, 2 pharate f, 12 c 10 paratype f, mature e composite of types composite of types	ANIC, BME ANIC, BME ANIC, BME NZA NZAC BPBM, ANIC BPBM, ANIC	EU746817	EU746849 EU746919		
<i>M. nelsonensis</i> (Hoy)	02-177j	<i>N. fusca</i> <i>N. menziesii</i> <i>N. menziesii</i> <i>N. cumminghamii</i> <i>N. cumminghamii</i> <i>N. gumtii</i> , <i>N. moorei</i> <i>N. moorei</i> <i>N. fusca</i> , <i>N. menziesii</i> <i>N. menziesii</i> <i>N. menziesii</i> <i>N. fusca</i> <i>N. fusca</i>	MC, Banks Peninsula, Hinewai Res. New Zealand SL, Owaka Australia Tasmania, Maydena Australia NSW, New England NP New Zealand TO, Ohakune, Moore St NN, Kahurangi NP New Zealand BR, St Arnaud, Lake Rotoiti	4 f, 2 pharate f, 12 c 10 paratype f, mature e composite of types composite of types	NZA NZAC BPBM, ANIC BPBM, ANIC			EU746825 EU746886 EU746855	
<i>M. nothofagi</i> (Hoy)	58/41	<i>N. menziesii</i> <i>N. menziesii</i> <i>N. cumminghamii</i> <i>N. cumminghamii</i> <i>N. gumtii</i> , <i>N. moorei</i> <i>N. moorei</i> <i>N. fusca</i> , <i>N. menziesii</i> <i>N. menziesii</i> <i>N. menziesii</i> <i>N. fusca</i> <i>N. fusca</i>	MC, Banks Peninsula, Hinewai Res. New Zealand SL, Owaka Australia Tasmania, Maydena Australia NSW, New England NP New Zealand TO, Ohakune, Moore St NN, Kahurangi NP New Zealand BR, St Arnaud, Lake Rotoiti	4 f, 2 pharate f, 12 c 10 paratype f, mature e composite of types composite of types	NZA NZAC BPBM, ANIC BPBM, ANIC			EU746825 EU746886 EU746855	
<i>M. occultus</i> , sp. nov.	NZ4 LGC162	<i>N. menziesii</i> <i>N. menziesii</i> <i>N. cumminghamii</i> <i>N. cumminghamii</i> <i>N. gumtii</i> , <i>N. moorei</i> <i>N. moorei</i> <i>N. fusca</i> , <i>N. menziesii</i> <i>N. menziesii</i> <i>N. menziesii</i> <i>N. fusca</i> <i>N. fusca</i>	MC, Banks Peninsula, Hinewai Res. New Zealand SL, Owaka Australia Tasmania, Maydena Australia NSW, New England NP New Zealand TO, Ohakune, Moore St NN, Kahurangi NP New Zealand BR, St Arnaud, Lake Rotoiti	4 f 1 f 2 f (1 for DNA)	ANIC ANIC ANIC	EU746829		EU746870	
<i>M. papillosus</i> (Hoy)	LGC157	<i>N. fusca</i> <i>N. fusca</i>	BR, St Arnaud, Lake Rotoiti	2 f (1 for DNA)	ANIC	EU746825 EU746886 EU746855			

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Appendix I. (continued)

Species [new names in bold]	Code	Hosts	Collection locality (*indicates not part of natural range)	Morphology	Depository	18S	EF-1 α	28S	wg
<i>M. pulchellus</i> (Maskell)		<i>N. solandri</i>	New Zealand						
	LGC160	<i>N. solandri</i>	BR, 12 km S Lewis Pass	3 f	ANIC				
	LGC360	<i>N. solandri</i>	NC, Klondyke Corner	1 f	ANIC				
	Maskell #103	<i>N. solandri</i>	Maskell Coll., no locality	composite of types	NZAC, USNM				
<i>M. raitithyi</i> (Maskell)		<i>N. menziesii</i>	New Zealand						
		<i>N. menziesii</i>	Maskell Coll., no locality	Lectotype f, 1 pl f	NZAC				
<i>M. rhadinotrix</i> (Miller & González)		<i>N. dombeyi</i> , <i>N. nitida</i> , <i>N. obliqua</i>	Argentina, Chile						
		<i>N. dombeyi</i>	Arg., c. 60 km NW of Bariloche	4 f	ANIC				
		<i>N. nitida</i>	Ch., PN Alerce Andino	3 f	ANIC				
<i>M. rotundus</i> (Hoy)		<i>N. fusca</i> , <i>N. solandri</i> , <i>N. truncata</i>	New Zealand						
		<i>N. solandri</i>	NN, Stanley Brook	4 paratype f, mature eNZAC					
		<i>N. fusca</i>	New Zealand						
<i>M. rubrifagi</i> (Hoy)		<i>N. fusca</i>	TO, Rangataua	1 paratype f	NZAC				
		<i>N. fusca</i>	New Zealand						
<i>M. viridulus</i> Hoy	LGC161	<i>N. fusca</i> , <i>N. truncata</i>	NN/BR, 7 km E of Lyell	1 f	ANIC		EU746887	EU746871	
		<i>N. fusca</i>	BR, Rahu Saddle	1 f	NZAC				
		<i>N. fusca</i>	NN, Golden Bay	3 f	NZAC				
		<i>N. truncata</i>	NN, Whangamoa Saddle	1 f, 1 c	NZAC				
		<i>N. fusca</i>	NN, Nelson, Flora Saddle	1 f, 4 e	ANIC		EU746888	EU746872	
OUTGROUPS									
<i>Chilechiton lymnae</i> Hodgson & Miller		<i>Nothofagus dombeyi</i>	Chile	1 paratype f	USNM				
	LGC585	<i>N. antarctica</i>	PN Puyehue	6 f (1 for DNA)	ANIC, BME	EU746805	EU746889	EU746846	EU746923
	LGC348	<i>N. antarctica</i>	RN Villarrica	1 f	ANIC		EU746890	EU746845	
<i>Chilecoccus browni</i> Miller & González		<i>Nothofagus dombeyi</i>	Argentina, Chile						
		<i>N. dombeyi</i>	Arg., c. 60 km NW Bariloche	1 f	ANIC				
			Ch., Cautín, Camino a Villarrica	2 paratype f	BME				
<i>C. nr browni</i>		<i>Nothofagus dombeyi</i>	Chile						
	LGC580	<i>Nothofagus dombeyi</i>	PN Puyehue	3 f (1 for DNA)	ANIC, BME	EU746806		EU746847	EU746922
<i>Chilecoccus spinosus</i> Miller & González		<i>Nothofagus dombeyi</i>	Chile						
	LGC318	<i>Nothofagus dombeyi</i>	PN Nahuelbuta	2 f	ANIC	EU746807		EU746848	EU746921
	LGC350	<i>N. dombeyi</i>	PN Villarrica	1 f	ANIC				
<i>Eriochiton hoheriae</i> Hodgson		<i>Hoheria angustifolia</i>	New Zealand						
	LGC600		MC, Banks Pen., Prices Valley Res.		ANIC	EU746800		EU746834	EU746908
<i>Eriochiton spinosus</i> (Maskell)		<i>Griselinia littoralis</i>	New Zealand						
	Echit1		HB, Black Birch Range		ANIC	EU746799	EU746891	EU746833	EU746907
<i>Eriococcus aceris</i> (Signoret)		<i>Acer compestre</i>	Hungary						
	acer1		Budapest		ANIC	AY795539	EU746892	EU746830	EU746903
<i>E. araucariae</i> Maskell		<i>Araucaria heterophylla</i>	Colombia*						
	LGC357		Calí-Valle		ANIC			EU746832	

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Appendix 1. (continued)

Species [new names in bold]	Code	Hosts	Collection locality (*indicates not part of natural range)	Morphology	Depository	18S	EF-1 α	28S	wg
<i>E. arcanus</i> Hoy	LGC358	<i>Phyllocladus trichomanoides</i>	New Zealand ND, Paihia	3 f	ANIC	EU746809		EU746850	
<i>E. brittini</i> Hoy	LGC362	<i>Coprosma rotundifolia</i>	New Zealand WD, Haast Valley USA*	3 f (1 for DNA)	ANIC	EU746810		EU746851	EU746924
<i>E. coccineus</i> Cockerell	cocc1	<i>Mammillaria</i> sp. <i>Mammillaria priessnitzii</i>	MD, Prince Georges Co. store CA, Solano Co., Vacaville	2 f	ANIC BME	AY795536	EU746893	EU746831	EU746904
<i>E. phyllocladi</i> Maskell	LGC359	<i>Phyllocladus asplenifolius</i>	New Zealand TO, Tongariro NP	1 f	ANIC	EU746812		EU746843	
<i>E. tholothrix</i> Miller & González	LGC349 LGC382	<i>Eucryphia cordifolia</i> <i>E. cordifolia</i> <i>E. cordifolia</i>	Chile c. 20 km E Puerto Montt Villarrica PN Alerce Andino	4 f 1 f 3 f (1 for DNA)	ANIC ANIC ANIC, BME	EU746811 EU746813	EU746894 EU746895	EU746856 EU746857	EU746914 EU746915
<i>Icelococcus nothofagi</i> Miller & González	LGC583f2	<i>Nothofagus nitida</i>	Chile PN Puyehue, Anticura	4 f (1 for DNA)	ANIC	EU746801	EU746896	EU746837, EU746836	
EU746906		<i>N. dombeyi</i>	Hotel Petrohue Chile	3 f	BME				
<i>Intecicoccus viridis</i> Kondo	LGC317	<i>Nothofagus antarctica</i>	RN Villarrica Australia		ANIC	EU746808		EU746844	EU746920
<i>Lachnodius</i> sp.	lach4	<i>Eucalyptus</i> sp.	NSW, Wild Cattle Ck SF New Zealand		ANIC	AY795521	EU746897	EU746840	EU746909
' <i>Madarococcus</i> ' <i>totarae</i> (Maskell)		<i>Podocarpus totara</i>	MC, Christchurch,	1 f, > 6 e	NZAC				
' <i>M.</i> ' nr <i>totarae</i>		<i>P. totara</i>	AK, Waitakere Ra New Zealand	1 f, 1c	NZAC				
	totar1	<i>Podocarpus totara</i> <i>P. totara</i>	MC, Akaroa, Grehan Valley AK, Riverhead Forest, Barlow Rd Res.	1 f 5 f, 2 c	NZAC ANIC	AY795534	EU746898	EU746842	EU746913
<i>Opisithoscelis mammularis</i> Froggatt	mamm1	<i>Eucalyptus</i> ? <i>nortonii</i>	Australia NSW, Queanbeyan- Captains Flat Rd		ANIC	EU746803	EU746899	EU746839	EU746910
<i>Scutara lanuginosa</i>	Scut5	<i>Pseudopanax arboreus</i>	New Zealand TO, Mt Titirapunga Australia		ANIC	EU746802	EU746900	EU746835	EU746905
' <i>Sphaerococcus</i> ' <i>socialis</i> Maskell	soc1	<i>Melaleuca lateriflora</i> var. <i>acutifolia</i>	WA, Perth, Kenwick		ANIC	AY795527	EU746901	EU746838	EU746911
<i>Sitobococcus cerinus</i> Miller & González	LGC347	unident. Myrtaceae	Chile RN Villarrica		ANIC	EU746804	EU746902	EU746841	EU746912