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A new genus and two new species of felt scales (Hemiptera: Coccoidea: Eriococcidae) from Chile, with comments on zoogeographical affinities between the eriococcid faunas of southern South America and New Zealand

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Abstract. A new eriococcid genus (*Chilechiton* Hodgson & Miller) and the adult female, second-instar female and first-instar nymphs of two new species of Eriococcidae (*Chilechiton lynnae* on *Nothofagus* and *Icelococcus lithreae* on *Lithraea*) are described. *Chilechiton* is closely related to the New Zealand genus *Eriochiton* Maskell in tribe Eriochitonini, previously considered to be restricted to New Zealand. A phylogenetic analysis was undertaken to investigate the relationships of the Chilean and New Zealand eriococcid genera included in the study, the systematic boundaries of Eriochitonini and the relationship of Coccidae to Eriochitonini. The study suggests that the Chilean eriococcid fauna is closely related to that in New Zealand, Eriochitonini should be enlarged to include *C. lynnae*, genus *Eriococcus* is polyphyletic, Eriococcidae is monophyletic, and Coccidae and Eriococcidae are not closely related.

Introduction

Eriococcidae or felt scales are the fourth largest family of scale insects (Hemiptera: Sternorrhyncha: Coccoidea) and are most abundant in the Southern Hemisphere, especially in New Zealand (Hoy, 1962) and Australia. It is likely that they are also abundant in much of South America, but this continent has been little explored and few species are known from there. Indeed, prior to 1975, only two species had been recorded from Chile, but then Miller & González (1975) described four new genera and ten new species, mainly on *Nothofagus*. The paper by Miller & González drew attention to a number of features of the Chilean eriococcids that suggested a closer relationship with the eriococcids from New Zealand than with those from North America or even from northern South America. In addition, Miller & González highlighted a number of features that suggested that Eriococcidae and Coccidae might be closely related.

The present paper describes two additional eriococcid species from Chile. One is placed in the Chilean genus *Icelococcus* Miller & González, whereas the other is placed in a new genus that shows a remarkable similarity to the New Zealand genus *Eriochiton* Maskell. The latter genus was considered to belong to Coccidae by earlier workers (Maskell, 1887; Morrison & Morrison, 1922), but was recently transferred to Eriococcidae (Hodgson, 1994; Hodgson & Henderson, 1996) and placed in a new tribe, Eriochitonini. The *in situ* appearance of species of *Eriochiton* (Henderson & Hodgson, 1995) and a related genus, *Neoeriochiton* Hodgson (Hodgson, 1994), shows the general gestalt of a soft scale, being round in body outline, dorsoventrally flattened, with platelike anal lobes and little obvious dorsal wax. In addition, slide-mounted specimens share such soft scale characteristics as an anal cleft and an invaginated anal ring. However, detailed analyses of the morphology of slide-mounted adult females, adult males and first-instar nymphs (Hodgson, 1994; Henderson & Hodgson, 1995; Hodgson & Henderson, 1996; Miller & Hodgson, 1997) have shown that, notwithstanding the

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presence of these coccidlike characteristics, these unusual scales should be placed in Eriococcidae.

Despite the suggestion by Miller & González (1975) that Eriococcidae and Coccidae might be closely related, phylogenetic analyses of scale insect families (Boratyński & Davies, 1971; Miller & Miller, 1993b; Miller & Williams, 1995; Foldi, 1997; Miller & Hodgson, 1997) have not demonstrated this close relationship, even though genera such as *Eriochiton*, *Neoeriochiton*, *Icelococcus* Miller & González, *Chilecoccus* Miller & González, *Exallococcus* Miller & González and the new genus *Chilechiton* seem to possess character states suggesting that they are annectant taxa.

Two phylogenetic analyses were therefore undertaken. The main analysis aimed to look more closely at the relationships between certain eriococcid genera, concentrating on those from the Southern Hemisphere, and the second looked a little more closely at the relationship between Coccidae and Eriococcidae.

Materials and methods

In addition to the two new species, the main analysis included exemplars of taxa purported to be closely related to the eriococcids and coccids: Aclerdidae, *Aclerda arundinariae* McConnell; Asterolecaniidae, *Grammococcus adetocorymbus* Miller & Lambdin; Cerococcidae, *Cerococcus andinus* Leonardi; Coccidae, *Coccus hesperidum* Linnaeus; Eriococcidae, *Chilecoccus browni* Miller & González and *C. spinosus* Miller & González (Neotropical), *Eriochiton spinosus* (Maskell) and *E. hispidus* Maskell (New Zealand), *Eriococcus buxi* (Fonscolombe) (Palaearctic), *E. cavellii* (Maskell) (New Zealand); *E. coccineus* (Cockerell) (Holarctic), *E. eurythrix* Miller & González (Neotropical), *E. pohutukawa* Hoy (New Zealand), *E. quercus* (Comstock) (Holarctic) and *E. spurius* (Modeer) (Palaearctic), *Exallococcus laureliae* Miller & González (Neotropical), *Icelococcus nothofagi* Miller & González (Neotropical), *Madarococcus maculatus* (Maskell) (New Zealand), *Neoeriochiton clareae* Hodgson (New Zealand), *Noteococcus hoheriae* (Maskell), *Phloeococcus cordylinidis* Hoy and *P. loriceus* Hoy (New Zealand), *Scutare fimbriata* Brittin (New Zealand), *Stibococcus cerinus* Miller & González (Neotropical); Kermesiidae, *Eriokermes gillettei* Tinsley; Lecanodiaspididae, *Lecanodiaspis acaciae* (Maskell); Micrococcidae, *Micrococcus bodenheimeri* Bytinski-Salz; Pseudococcidae, *Pseudococcus longispinus* (Targioni Tozzetti); Kerriidae, *Tachardiella larreae* (Comstock). *Pseudococcus longispinus* was treated as the outgroup. The Holarctic and Palaearctic *Eriococcus* species were chosen because they had sclerotized anal lobes and other characters similar to those from Chile and New Zealand. Thus, a total of thirty-one taxa and forty-five characters were used in the main analysis.

The second, subsidiary, analysis included two additional coccid species from different subfamilies, *Luzulaspis americana* Koteja & Howell (Eriopeltinae; Nearctic) and *Eulecanium tiliae* (Linnaeus) (Eulecaniinae; Holarctic). In a previous cladistic analyses of Coccidae (Miller & Hodgson, 1997), Eriopeltinae and Eulecaniinae were found to be rather basal, whereas subfamily Coccinae (which contains *C. hesperidum*) was consistently at the apex of the cladogram. The three species are therefore considered to show a wide spectrum of soft scale characters.

Characters and character states are presented in Appendix 1; the character matrix is given in Appendix 2. Outgroup comparison was used to determine the polarity of characters and all multistate characters were treated as unordered. Phylogenetic analyses were performed with PAUP 3.1.1 (Swofford, 1993) and PAUP 4.0.0 (Swofford, 2000), using the heuristic search protocol with 1000 random-addition sequence replicates. The DELTRAN optimization criterion was selected for determining the character state of equivocal branches (Maddison & Maddison, 1992). A simple decay analysis was used by running a general heuristic search and keeping cladograms with 1, 2 and 3 steps more than the shortest cladograms. In most decay analyses, a strict consensus is used to show the structure of the resulting consensus cladogram, but, by using the strict consensus, a single deviant cladogram out of hundreds or even thousands of cladograms with uniform structure will eliminate the structure of the majority of the cladograms. To avoid this scenario, our decay analyses provide data not only for the strict consensus analysis but also for a 90% majority rule consensus. It does not make sense to us to eliminate the structure of a consensus cladogram that occurs in at least 90% of all the cladograms in the decay analysis. MacClade 3.01 (Maddison & Maddison, 1992) was used to study character distribution. Where character states were not available on the adult female (such as when the adult females are apodous), these were taken from the first-instar nymphs. Unfortunately, first-instar nymphs were not available for all species. However, based on our current state of knowledge of first-instar nymphs, we believe that the character states used in this study tend to be the same in the nymph as in the adult female.

Terminology in the descriptions below follows that of Miller & Miller (1993a) and Miller & McKenzie (1967). As the most definitive works on Eriochitonini are those of Hodgson (1994) and Hodgson & Henderson (1996), and the terminology used in these papers is most closely allied with descriptive characters of Coccidae, synonyms of terms as they are used in Eriococcidae and Coccidae are as follows: spinose setae (Coccidae) = enlarged setae (Eriococcidae); ventral microducts (Coccidae) or sessile pores (Eriochitonini) = cruciform or bilocularpores (Eriococcidae); disc-pores (Coccidae) = multilocular sessile pores (Eriococcidae); tubular ducts (Coccidae) = macrotubular ducts (Eriococcidae); coxal pores (Eriochitonini) = translucent pores (Eriococcidae); subapical seta (Coccidae) = posterior anal-lobe seta (Eriococcidae).

An additional term that needs clarification is 'suranal seta'. This term was used by Hoy (1962) as follows: 'On either side of the anal ring is, usually, a suranal seta. These setae are generally slender and tapering, but in a number of species, usually those associated with the tree genus *Nothofagus*, they are broad and spatulate, often much wider at the apex than at the base.' In eriococcid genera such as *Eriococcus*, this seta is homologous to the antero-

ventral seta of the anal lobe. In *Eriococcus,* there is a second seta on the lobe that is just anterior to the subapical or posterior anal-lobe seta. Similar setae, identical to those on species from New Zealand, were described by Miller & González (1975) on *Eriococcus eurythrix* off *Nothofagus antarctica* from Chile. However, while describing various *Eriochiton* species, Hodgson & Henderson (1996) found a spatulate seta on the ventral surface of the anal plates and referred to it as the suranal seta. On closer examination, it is now apparent that this seta is not the suranal seta as defined by Hoy (1962) but is homologous to the seta on *Eriococcus* species that occurs on the ventral surface just anterior to the posterior seta. Because the anal ring in Eriochitonini is frequently invaginated, the true suranal setae on species of Eriochitonini rest on the anal fold and are not spatulate. To clarify the names of these setae, we use the terms 'anterior suranal seta' for the setae near the anal opening and 'posterior suranal seta' for the setae on the ventral surface of the anal plates. Therefore, the seta that is spatulate on many *Nothofagus*-infesting species in New Zealand is here called the 'anterior suranal seta' and the seta that is spatulate or enlarged in species of *Eriochiton* and *Neoeriochiton* is here called the 'posterior suranal seta' (Fig. 1).

HT and PT refer to holotype and paratype specimens, respectively; measurements and numbers are from all available specimens and are given as an average followed by the range in parentheses. Enlargements on illustrations are not proportional. Depository abbreviations are as follows: Australian National Insect Collection, CSIRO, Canberra (ANIC); The Bohart Museum, University of California, Davis (UCD); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Beltsville, MD (USNM); The Natural History Museum, London (BMNH); University of Chile, College of Agriculture, Santiago (UCH).

Key to adult females of genera and species of Eriococcidae known from Chile (modified after Miller & González, 1975)

1. Macrotubular ducts absent from dorsum 2
– Macrotubular ducts present on dorsum 5
2(1). Anal lobes in form of plates, withdrawn onto dorsal surface at anterior end of an anal cleft; anal tube present; ventral cruciform pores absent ..... *Chilechiton lynnae*
– Anal lobes in form of lobes heavily sclerotized but not withdrawn onto dorsum; anal cleft absent; anal tube absent; ventral cruciform pores present (*Icelococcus*) 3
3(2). Hind coxae without translucent pores; dorsal setae of one size ..... *I. lithreae*
– Hind coxae with numerous large translucent pores; dorsal setae of 2 sizes 4
4(3). Macrotubular ducts present on venter; hind coxae not greatly expanded ..... *I. charlini*
– Macrotubular ducts absent from venter; hind coxae greatly expanded ..... *I. nothofagi*
5(1). Macrotubular ducts on dorsum each with conspicuous rim around dermal orifice 6
– Macrotubular ducts on dorsum without a conspicuous rim around dermal orifice 7
6(5). Venter with large clusters of macrotubular ducts on abdomen; dorsum without simple pores; cruciform pores absent ..... *Stibococcus cerinus*
– Venter without macrotubular ducts on abdomen; dorsum with numerous simple pores; cruciform pores present on venter near body margin ..... *Exallococcus laureliae*
7(5). Enlarged setae unusually abundant, present ventrally on all areas of abdomen; anal lobes modified into platelike structures (*Chilecoccus*) 8
– Enlarged setae not abundant; when present, restricted to lateral areas of venter of abdomen; anal lobes unmodified, not platelike 9
8(7). Multilocular sessile pores absent from dorsum, restricted to narrow, longitudinal band on mediolateral areas of venter; dorsal surface of each hind coxa with 65–120 pores ..... *C. browni*
– Multilocular sessile pores abundant on dorsum as well as on mediolateral and lateral areas of venter; dorsal surface of each hind coxa with 35–65 pores ..... *C. spinosus*
9(7). Dorsal setae each dome-shaped; hind femora each with 4 setae ..... *E. tholothrix*
– Dorsal setae each not dome-shaped; hind femora each with 5 setae 10
10(9). Anterior suranal setae spatulate; femora of front legs each with 6 setae ..... *E. eurythrix*
– Anterior suranal setae bristle-shaped; femora of front legs each with fewer than 6 setae 11
11(10). Dorsomedial enlarged setae each truncate apically; ventral multilocular sessile pores on thorax each usually with 3 loculi; tibiae of front legs each with 5 setae ..... *E. araucariae*
– Dorsomedial enlarged setae each with an acute or rounded apex; ventral multilocular sessile pores on thorax each usually with 5 loculi; tibiae of front legs each with 4 setae 12
12(11). Dorsomedial setae on abdomen each about equal in length to largest lateral setae ..... *E. chilensis*
– Dorsomedial setae on abdomen each noticeably smaller than largest lateral setae 13
13(12). Antennae each 6-segmented; abdominal segment V with 9–14 enlarged setae; ratio of hind tibia to hind tarsus 0.7–0.8 : 1; enlarged setae on dorsomedial areas of thorax and head each about same size as those along margin of abdomen .... *E. rhadinothrix*
– Antennae each 7-segmented; abdominal segment V with 19–31 enlarged setae; ratio of hind tibia to hind tarsus 0.9–1.1 : 1; enlarged setae on dorsomedial areas of thorax and head each noticeably smaller and more slender than those along margin of abdomen ..... *E. navarinoensis*

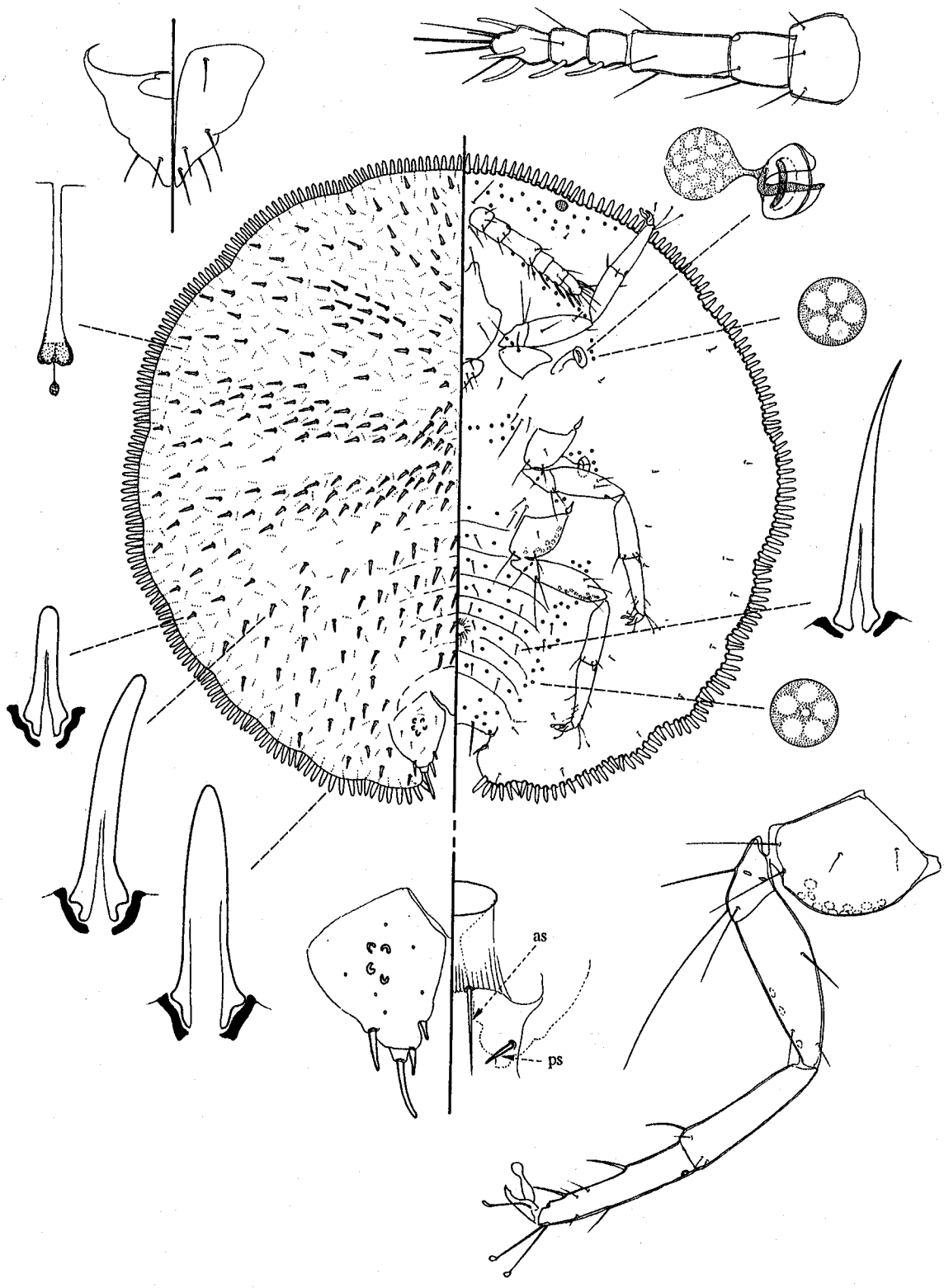

Fig. 1. *Chilechiton lynnae*, adult female. Left half of main drawing showing dorsal characters, right half ventral. Vignettes of structures not shown to the same scale. as = anterior suranal seta; ps = posterior suranal seta.

Chilechiton Hodgson & Miller, gen.n.

Type species: *Chilechiton lynnae* Hodgson & Miller

Generic diagnosis. Adult female (Fig. 1). *Dorsum*: Body outline nearly round. Derm membranous, possibly becoming mildly sclerotized at maturity. Setae of enlarged type only; setose setae lacking. Microtubular ducts present; without other kinds of pores or ducts. With 2 lateral, heavily sclerotized, platelike anal lobes, when together, quadrate; each with pointed apices, withdrawn onto dorsal surface; each lobe with microtubular ducts, 4 enlarged setae on margins and C-shaped or irregular indentations on dorsal surface. Third plate present anteromedially between lateral platelike anal lobes, barely recognizable, unsclerotized.

Margin: Marginal enlarged setae similar to setae on dorsum but generally smaller; margin of anal cleft without marginal setae. Anal ring located between anal lobes, with 2 incomplete rows of pores and 8 basally enlarged setae. Anal cleft present.

Venter: Derm membranous. Multilocular sessile pores each usually with 5 loculi; present in medial and mediolateral areas of abdomen. Preantennal pores present. Cruciform pores, macrotubular ducts and microtubular ducts absent. With 3 pairs of setae between antennae, arranged more or less in 2 longitudinal lines. Eyespots located submarginally, laterad of antennal base. Legs well developed, translucent pores represented by large areas of thinner cuticle on hind leg segments. Each leg with tibia shorter than tarsus; tarsus with campaniform sensillum; claw with denticle; tarsal digitules capitate, about equal in size; claw digitules with one conspicuously swollen, other about same size as a tarsal digitule; femur with 5 setae; each meso- and metatibia with 4 setae but each protibia with 5. Antennae each 6-segmented. Labium 3-segmented; basal segment very small, represented by a small sclerotized plate partially or completely fused with second segment, bearing 1 or 2 pairs of setae; second segment large, with one pair of setae; third segment large, separated from second segment by small constriction, bearing 5 pairs of setae. Opening of vulva situated between segments VI and VII. Anterior suranal setae simple and unmodified. Posterior suranal setae enlarged.

Second-instar female (Fig. 2). Similar to adult female but with fewer setae and pores, body and appendages are smaller and anal ring with 6 setae.

First-instar nymph (gender not determined) (Fig. 3). *Dorsum*: Anal cleft absent. Derm membranous. Setae of 2 sizes, both enlarged types: largest type arranged in conspicuous submedial and mediolateral longitudinal lines; smallest type present in mediolateral areas of posterior abdominal segments. Microtubular ducts present; other kinds of pores or ducts absent. With 2 lateral, platelike, heavily sclerotized anal lobes placed on either side of anal ring, each with a longitudinal fold and with pointed apices; when together, quadrate; each with microtubular ducts and enlarged setae; posterior seta elongate. Third anteromedial plate absent.

Margin: Marginal enlarged setae present. Anal ring located between anal lobes, with 2 incomplete rows of pores and 6 basally enlarged setae.

Venter: Derm membranous. Multilocular sessile pores present; spiracular multilocular sessile pore bands absent. Preantennal pore present near base of each antenna. Cruciform pores and macrotubular ducts absent. With 3 pairs of setae on ventral mid-line of head between antennae, more or less in 2 longitudinal lines. Eyespots located submarginally, each laterad of antennal base. Legs well developed; each with tibia shorter than tarsus; tarsus with campaniform sensillum; claw with denticle; tarsal digitules capitate, about equal in size; claw digitules with one conspicuously swollen, other about same size as a tarsal digitule. Antennae each 6-segmented. Labium 3-segmented; basal segment very small, represented by a small sclerotized plate partially or completely fused with second segment, bearing 1 or 2 pairs of setae; second segment large, with 1 pair of setae; third segment large, separated from second segment by small constriction, bearing 5 pairs of setae. Anterior suranal seta with small sclerotization basally. Posterior suranal seta unmodified and setose.

Note. Adult females of *Chilechiton* are similar to those of *Eriochiton* and *Neoeriochiton* in having the vulva situated between segments VI and VII, macrotubular ducts absent, abdominal multilocular sessile pores arranged in mediolateral lines on abdomen, a distinct anal cleft, an invaginated anal ring, the labium appearing two-segmented but with a small additional basal third segment, four setae on each meso- and metatibia but with five setae on the protibia and five setae on each femur. The genera may be separated by *Chilechiton* having (condition on *Eriochiton* and *Neoeriochiton* in brackets) six-segmented antennae (seven-segmented); no multilocular sessile pores between the anterior spiracle and the body margin (multilocular sessile pores present), no setose dorsal setae (present or absent), no cruciform pores (many present ventrally near body margin), a pattern of C-shaped or irregular marks on the anal lobes (such marks absent), one claw digitule enlarged and the other not (claw digitules similar in size), posterior suranal setae enlarged, not spatulate (enlarged or spatulate), multilocular sessile pores spread over medial and mediolateral areas of abdominal venter (only present on mediolateral areas of abdomen, absent from medial areas), and no enlarged marginal setae on margins of anal cleft (present). Adult female *Chilechiton* are also similar to those of *Icelococcus* Miller & González because both have the vulva situated between segments VI and VII, a medial plate located dorsad of the anal ring, a similar arrangement of dorsal and marginal enlarged setae and large indistinct translucent pores. *Chilechiton* differs from *Icelococcus* in having (condition in *Icelococcus* in brackets) cruciform pores absent (present on venter near body margin), anal lobes developed into anal platelike structures (anal lobes lobelike, protruding posteriorly), anal ring invaginated

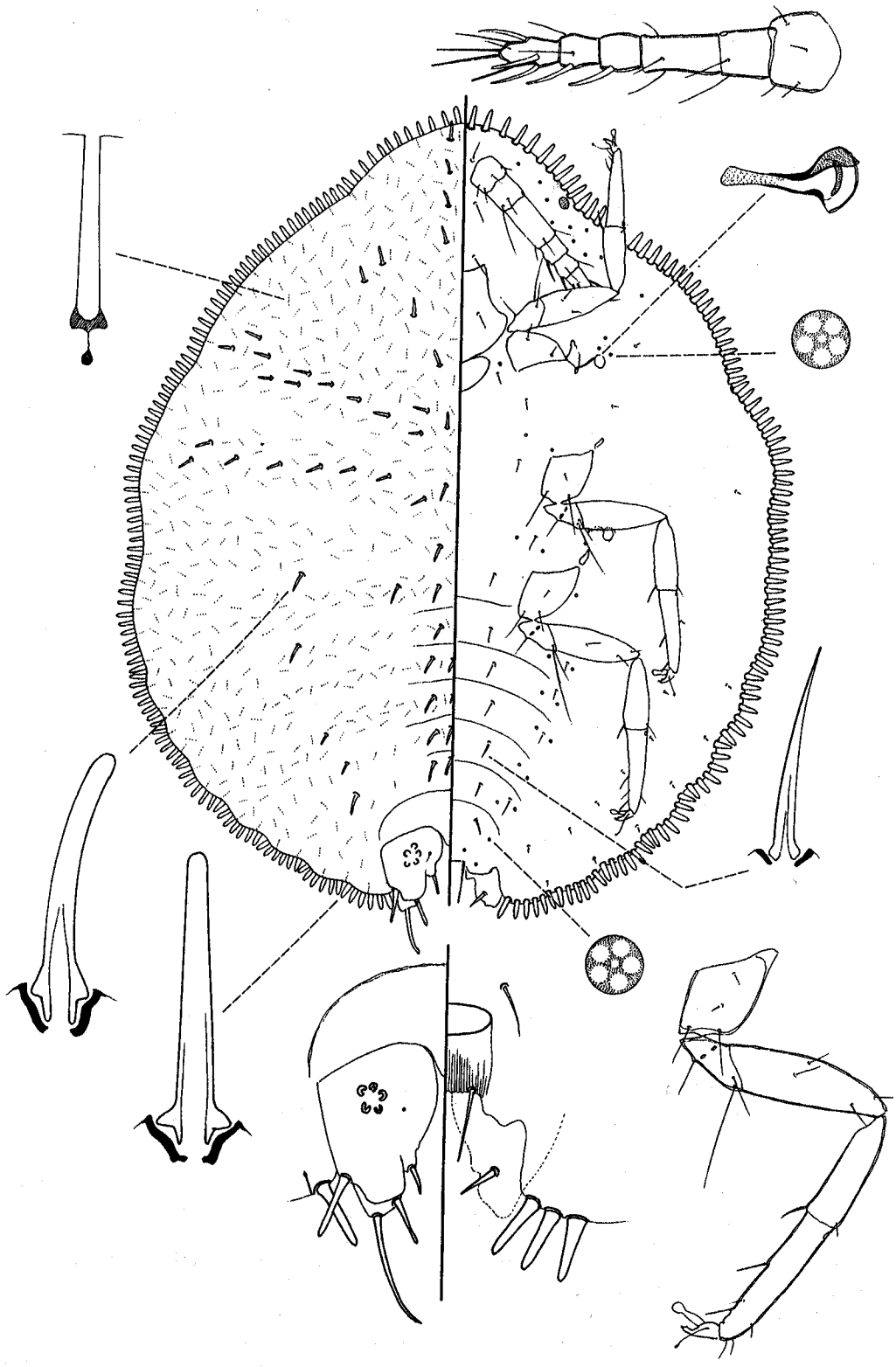

Fig. 2. *Chilechiton lynnae*, second-instar female.

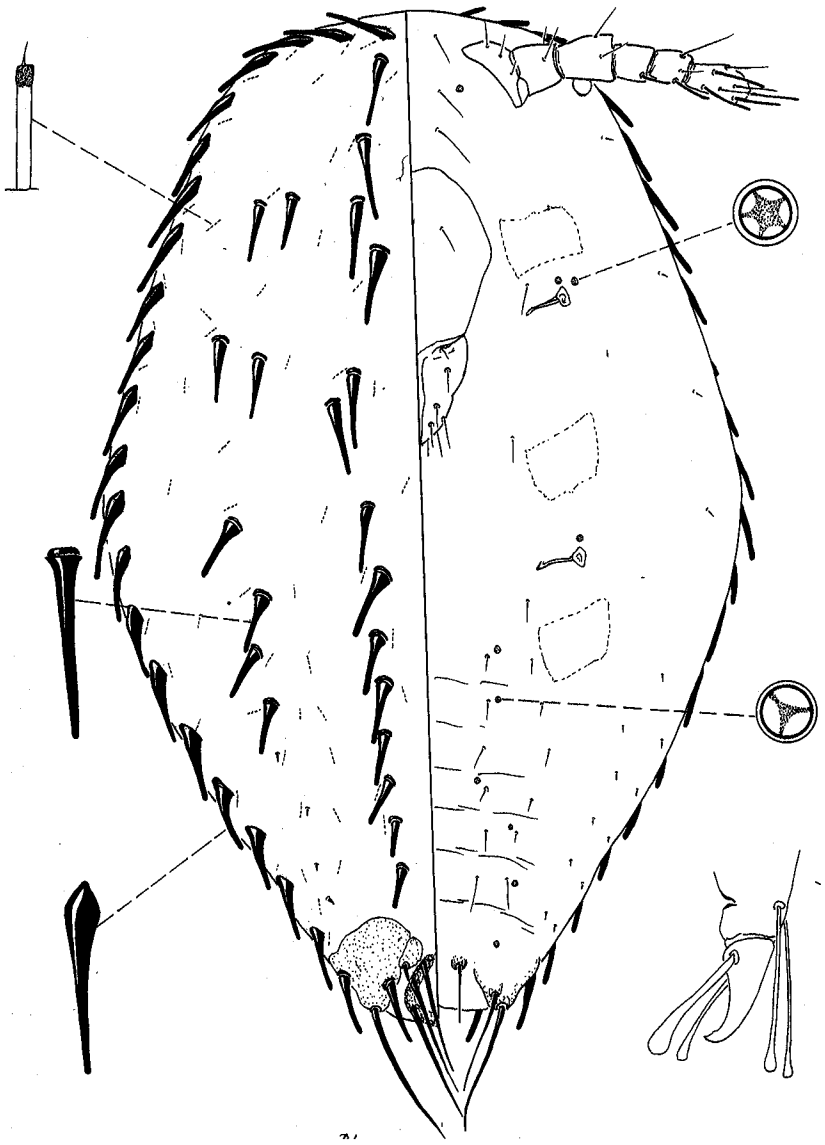

Fig. 3. *Chilechiton lynnae*, first-instar nymph. This illustration was made from embryos and the legs were insufficiently well sclerotized to illustrate.

(not invaginated) and one claw digitule swollen and conspicuously larger than the other (claw digitules of equal size).

Second-instar females of *Chilechiton* are similar to those of *Eriochiton* and *Neoeriochiton* in having the same arrangements of dorsal enlarged setae, microtubular ducts and multilocular sessile pores. The genera may be separated by *Chilechiton* having (condition on *Eriochiton* and *Neoeriochiton* in brackets) claw digitules of unequal size (equal size), cruciform pores absent (present), a pattern of C-shaped or irregular marks on the lateral anal lobes (marks absent), both pairs of suranal setae unmodified (posterior suranal setae spatulate or enlarged) and multilocular sessile pores absent from between the anterior spiracles and margin (present).

First-instar nymphs of *Chilechiton* have many similarities with other members of Eriochitonini, including a conspicuous row of marginal setae, platelike anal lobes, a total of seven setae present on each side of labium, four setae on each meso- and metatibia, but five on each protibia, five setae on each femur and simple microtubular ducts. First-instar *Chilechiton* differ from those of other Eriochitonini in having (condition in other Eriochitonini in brackets) claw digitules of two sizes (of one size), platelike anal lobes with longitudinal fold (longitudinal fold absent from both lobes), marginal setae with an asymmetrical base (base symmetrical) and both pairs of suranal setae unmodified (posterior suranal setae spatulate or enlarged).

Etymology. The name of this genus is formed from Chile, the country where it was collected, and the Greek noun *chiton* meaning tunic or garment worn next to the skin. *Chilechiton* is a masculine noun.

Chilechiton lynnae Hodgson & Miller, sp.n.

Type material. The holotype adult female is the specimen on the right of two mounted on a slide with the following information: right label 'CHILE: Malleco/Captren, n. Volcán/ Lliama, 50 km E./Temuco, Parque/Nacional Conguillio/ I-13-1989, on/*Nothofagus dombeyi*/L. S. Kimsey'; left label '*Chilechiton lynnae*/Hodgson & Miller/ HOLOTYPE &/ PARATYPE/ucd' and includes a map giving the position of the holotype (UCD). Paratype slides: in addition to paratype specimen on holotype slide, three slides containing three paratypes adult female plus a second-instar female nymph, with the same collection data as the holotype; one adult female contains nineteen first-instar embryos (BMNH, UCH, USNM).

Adult female (Fig. 1) (description based on 4 specimens). *Mounted material*: With shallow anal cleft. Total body length: HT 0.9 mm, PT 1.7 (1.0–2.5) mm; width: HT 1.0, PT 1.8 (1.1–2.6) mm.

Dorsum: Enlarged setae (excluding marginal setae) slightly curved, of one size, arranged in segmental rows over most of surface; longest seta: HT 20 μm, PT 26 (22–30) μm. Anal lobes platelike, each lobe with enlarged seta on each outer margin, HT 25 μm long, PT 21 (20–23) μm; anterior seta on inner margin, HT + PT 10 μm long; posterior seta on inner margin, HT 26 μm, PT 25 (23–28) μm long; each posterior suranal seta slightly enlarged, HT 37 μm, PT 36 (25–47) μm long; also with 4 or 5 microtubular ducts on each lobe of HT, PT with 3 (1–5) ducts and several C-shaped or irregular indentations on each lobe; lobe length: HT 119 μm, PT 126 (124–127) μm; lobe width: HT 94 μm, PT 88 (79–99) μm. Medial plate ill-defined but present.

Margin: Marginal setae each straight, with a slightly rounded apex; longest seta: HT 27 μm, PT 30 (27–32) μm; with 28 marginal setae between eyespots on HT, 31 (30–31) on PT; marginal setae absent from margins of anal cleft. Anal ring not always invaginated; width: HT 54 μm, PT 49 μm; longest anal-ring seta: HT 109 μm long, PT 92 (82–109) μm; ratio of length of longest anal-ring seta/width of anal ring: HT 2.0:1, PT 1.9 (1.7–2.2):1.

Venter: Multilocular sessile pores each normally with 5 loculi, rarely 6 or 7; present in 2 broad bands in medial and mediolateral areas from anal area to anterior abdominal segments, in medial area of mesothorax, near spiracles and on anterior apex of head. Spiracular multilocular sessile pore bands absent. Ventral setae arranged segmentally. Anterior suranal seta: HT 47 μm long, PT 46 (40–52) μm. Width of each eyespot: HT 15 μm, PT 16 (15–17) μm. Width of spiracular peritreme: HT 25 μm, PT 34 (31–35) μm. Legs with translucent pores on each metathoracic coxa and femur; measurements of hind leg: trochanter + femur: HT 146 μm, PT 158 (153–161) μm; tibia: HT 86 μm, PT 91 (88–94) μm; tarsus: HT 94 μm, PT 101(99–104) μm; ratio of tibia to tarsus: 0.9 : 1; ratio of trochanter + femur to tibia: HT 1.7 : 1, PT 1.7 (1.7–1.8):1.

Antennae: Length HT 193 μm, PT 220 (212–227) μm.

Labium: Length HT 47 μm, PT 65 (62–69) μm.

Second-instar female (Fig. 2) (description based on one specimen). *Mounted material*: Body oval, with very short anal cleft. Total body length 0.9 mm; width 0.6 mm.

Dorsum: Enlarged setae (excluding marginal setae) slightly curved, of one size, arranged in segmental rows, with 3 pairs of setae on each abdominal segment; each thoracic segment with row of up to 24 setae; head with double row of setae near midline; longest seta 27 μm. Anal lobes platelike, each with enlarged seta on outer margin 29 μm long; anterior seta on inner margin of lobe 11 μm long; posterior seta on inner margin of lobe 30 μm long; posterior suranal seta slightly enlarged, 37 μm long; also, each lobe with one microtubular duct and several C-shaped or irregular indentations; lobe length 70 μm; lobe width 57 μm. Medial plate ill-defined but present.

Margin: Marginal setae each straight, with a slightly rounded apex; longest seta 27 μm; with 23 marginal setae anteriorly between eyespots; marginal setae absent from margins of anal cleft. Anal ring situated at inner end of anal tube; width 41 μm; longest anal-ring seta 72 μm; ratio of length of longest anal-ring seta to width of anal ring 1.8 : 1.

Venter: Multilocular sessile pore distribution as on adult female, but with fewer pores and with none situated medially on mesothorax. Ventral setae arranged segmentally on abdomen; anterior suranal seta 52 μm long. Width of each eyespot 12 μm. Width of each spiracular peritreme 15 μm. Legs without translucent pores; measurements of hind leg: trochanter + femur 106 μm; tibia 61 μm; tarsus 82 μm; ratio of tibia to tarsus 0.7 : 1; ratio of trochanter + femur to tibia 1.7 : 1. Antennae each 6-segmented; length 151 μm. Labium length 47 μm.

First-instar embryo (gender not determined) (Fig. 3) (description based on 19 embryos inside of body of one adult female). *Mounted material*: Body oval. Total body length 0.5 (0.4–0.5) mm; width 0.3 mm.

Dorsum: Enlarged setae (excluding marginal setae) straight or slightly curved, of 2 sizes, arranged in 2 pairs of longitudinal lines, one pair submedial and one pair mediolateral; small setae present at posterior end of mediolateral line, with 1–5 in each line; large setae conspicuous, slightly longer than marginal setae, longest seta 46 (37–52) μm. Microtubular ducts scattered. Anal lobes platelike, each with a longitudinal fold separating anterior seta on inner margin from rest of lobe; anterior seta on inner margin of anal lobe situated on a small protrusion; enlarged seta on outer margin of each anal lobe 34 (29–37) μm long; anterior seta on inner margin 15 (11–17) μm, posterior seta on inner margin 41 (30–44) μm, posterior suranal seta

hairlike, 107 (99–123) μm; also, each lobe with 1 or 2 microtubular ducts and several C-shaped or irregular indentations; lobe length 41 (35–46) μm; lobe width 41 (37–44) μm. Medial plate absent.

Margin: Marginal enlarged setae each slightly smaller than a dorsal seta, curved, with anteriorly enlarged setal base, apex slightly rounded, pointing posteriorly; longest seta 41 (37–43) μm; 8 marginal setae present between eyespots. Anal ring without anal tube; width 34 (33–35) μm; longest anal-ring seta 68 (61–77) μm long; ratio of length of longest anal-ring seta to width of anal ring 1.8 (1.7–2.0):1.

Venter: Multilocular sessile pores few, restricted to mediolateral areas of abdomen, those on posterior segments normally each with 5 loculi and those on anterior abdominal segments each with 3 loculi; multilocular sessile pores also present near each spiracle and each antennal base. Ventral microtubular ducts absent. Ventral setae arranged segmentally. Width of each spiracular peritreme 9 (8–10) μm. Measurements of hind legs: trochanter + femur 72 (67–74) μm; tibia 32 (30–32) μm; tarsus 48 (47–49) μm; ratio of tibia to tarsus 0.7 (0.6–0.7):1; ratio of trochanter + femur to tibia 2.3 (2.1–2.5):1. Antennae each 125 (119–135) μm long. Labium 45 (42–52) μm long.

Note. Because the above description and illustration were derived from embryos, and because structures such as the legs are incompletely sclerotized, some of the measurements may be inaccurate.

Remarks and discussion. The first-instar nymphs of *C. lynnae* are very similar to those of *Exallococcus laureliae* in having conspicuous enlarged dorsal setae, anal lobe each with a longitudinal fold, multilocular sessile pores restricted to the mediolateral areas of the venter, posterior suranal setae unmodified and anterior suranal setae with basal dermal sclerotization. First-instar nymphs of *C. lynnae* differ from those of *E. laureliae* in having (condition on *E. laureliae* in brackets) claw digitules of unequal sizes (equal); cruciform pores absent (present along ventral submargin); simple pores absent (present on dorsum); four setae on each meso- and metatibia, but with five setae on each protibia (two setae on each tibia); five setae on each femur (two setae on each femur); and marginal setae with asymmetrical setal bases (symmetrical).

While studying embryos of this species, it became evident that sometimes the eggs still attached to the embryos had a series of small, sclerotized projections on the anterior end of the chorion. We have only observed these structures in eriococcids, although Stickney (1934) mentions spines on the eggs of halimococcids.

We also examined a single first-instar nymph that probably represents a second, undescribed, species of *Chilechiton*. It is from Aysen-Coyhaique, Fundo Los Coigiier, Chile, on *Nothofagus pumilio*. This specimen was 'collected' from herbarium specimens in the USNM. It is similar to *C. lynnae* in having asymmetrical marginal setae, two sizes of claw digitule, microtubular ducts and multilocular sessile pores of similar structure and distribution, five setae on each femur and four setae on each meso- and metatibia but with five setae on each protibia. This undescribed species differs in lacking large-sized enlarged setae on the dorsum in the submedial and mediolateral areas, these being replaced by small-sized enlarged setae.

Etymology. This species is named in honour of Lynn Kimsey (Department of Entomology, University of California, Davis). On 13 January 1989, Lynn was collecting Hymenoptera in the Parque Conguillio, southern Chile. She was a little discouraged with the quality and quantity of the wasps that she found because the area was covered with volcanic ash from a recent eruption of a nearby volcano. However, in the middle of an 'ash' flow, she discovered a sapling of southern beech, *Nothofagus dombeyi*, that was covered with hundreds of scale insects. Not only did she collect this interesting new species, but she also spends considerable time and effort improving the large Coccoidea insect collection at the University of California, Davis.

Icelococcus Miller & González, 1975

Type species: *Icelococcus nothofagi* Miller & González.

Generic diagnosis. Adult female. Anal lobes heavily sclerotized and rugose, with many medial teeth. Triangular plate present on dorsum anterior to anal lobes. Macrotubular ducts entirely absent or absent from dorsum. Microtubular ducts scattered over dorsum. Cruciform pores present along submargin of venter. Multilocular sessile pores primarily quinquelocular, restricted to venter. Labium distinctly 3-segmented (Miller & González, 1975).

Icelococcus lithreae Hodgson & Miller, sp.n.

Type material. The holotype adult female is mounted alone on a slide with the following information: Left label '*Lithraea caustica* Hook/Parque Nacional/la Campana/Olmué (Sector la Represa)/Chile/I-29-1986/E. Zuniga'; right label '*Icelococcus lithreae*/Hodgson & Miller/HOLOTYPE' (UCH). Paratype material: sixteen other slides containing thirty adult females, three second-instar female, four first instars and three first-instar embryo paratypes with the same collection data as the holotype (ANIC, BMNH, MNHN, UCD, UCH, USNM).

Adult female (Fig. 4) (described from 30 specimens). *Mounted material*: Anal cleft. Total body length: HT 1.6 mm, PT 1.8 (1.5–2.1) mm; width: HT 1.1, PT 1.2 (1.1–1.4) mm. Derm membranous, without nodules.

Dorsum: Enlarged setae slightly curved, of one size, arranged in segmental rows over most of surface; longest

seta: HT 62 μm, PT 65 (62–72) μm. Microtubular ducts each with inner longitudinal line, and with small apical piece at derm surface, and longer basal piece, sclerotized throughout; scattered over surface. Anal lobes sclerotized and triangular when orientated with dorsal surface facing up but in life probably lying on edge, with inner margins ventral and with series of conspicuous teeth on ventral margin; anal-lobe setae difficult to analyse, when properly orientated, each lobe with a total of 7 or 8 setae, including anterior suranal seta and elongate posterior suranal seta; each lobe with 3 or 4 microtubular ducts on HT, 3 (1–5) on PT; lobe length: HT 170 μm, PT 169 (150–182) μm; lobe width: HT 88 μm, PT 102 (88–115) μm. Medial plate triangular, sclerotized, normally with one microtubular duct and nodulose surface. Sclerotized rectangular plate present anterior to medial plate on dorsal surface, containing several microtubular ducts.

Margin: Without distinct marginal row of setae. Anal ring invaginated between dorsal and ventral surface; ring bearing a single row of pores and 4 pairs of setae; anal tube inconspicuous; width of anal tube: HT 55 μm, PT 55 (48–62) μm; length of longest anal-ring seta: HT 140 μm, PT 126 (95–140) μm; ratio of length of longest anal-ring seta to width of anal ring: HT 2.5 : 1, PT 2.3 (2.0–2.5):1.

Venter: Multilocular sessile pores each normally with 5 loculi, rarely with 3, 4 or 6; present in 2 broad bands in

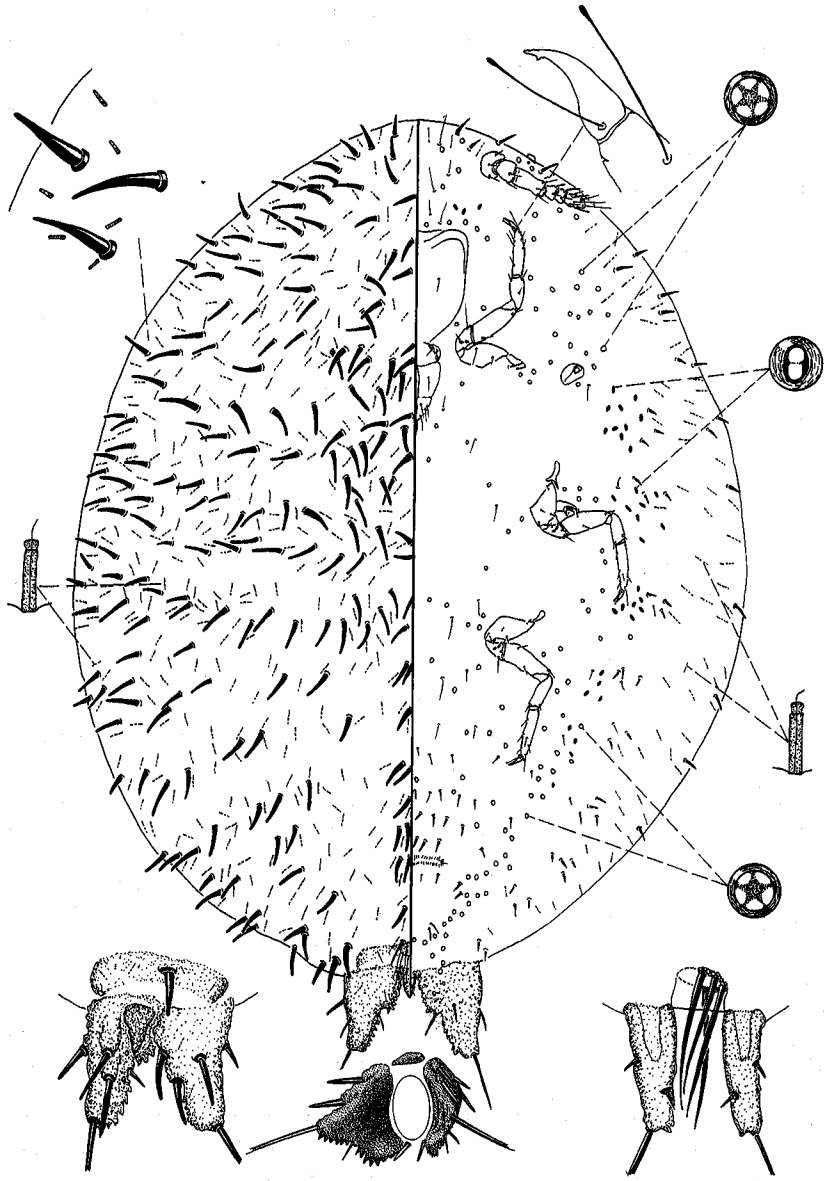

Fig. 4. *Icelococcus lithreae*, adult female. The vignette of the anal lobes on the left is as seen on the holotype slide, that on the right is how the lobes appear on another specimen, probably a dorsal view, and the middle vignette is as the authors feel it may appear in life, with the lobes lying vertically on either side of the anal opening.

mediolateral areas from anal area to head, forming segmental rows on anterior abdominal segments and scattered in medial areas of thorax, near spiracles and on anterior apex of head; spiracular multilocular sessile pore bands absent. Cruciform pores present in clusters in mediolateral areas laterad to multilocular sessile pores on anterior abdominal segments and thorax, and anterior to clypeus. Microtubular ducts present near body margin. Ventral setae arranged segmentally, slightly enlarged posteriorly; anterior suranal seta enlarged, length: HT 32 μm, PT 31 (28–38) μm; posterior suranal seta also enlarged. Width of each eyespot: HT 20 μm, PT 20 (18–22) μm. Width of spiracular peritremes: HT 18 μm, PT 19 (15–20) μm. Legs without translucent pores; measurements of hind leg: trochanter + femur: HT 130 μm, PT 122 (108–132) μm; tibia: HT 62 μm, PT 58 (52–62) μm; tarsus: HT 98 μm, PT 96 (92–100) μm; ratio of tibia to tarsus 0.6 : 1; ratio of trochanter + femur to tibia: HT 2.1 : 1, PT 2.1 (2.0–2.3):1. Femur with 5 setae; each meso- and metatibia with 4 setae but each protibia with 5 setae; tarsal digitules clubbed, equal in size on all legs; claw digitules slightly clubbed, equal in size; claw with denticle.

Antenna: Length HT 202 μm, PT 196 (180–208) μm.

Labium: Length HT 120 μm, PT 124 (112–138) μm; segment 1 represented by a small sclerotized strip with 2 pairs of setae on each side of segment; segment 2 with a single seta on each side; segment 3 bearing 7 pairs of setae, 2 pairs of them situated on dorsal surface.

Note. The anal lobes seem to have a definite three-dimensionality that is difficult to interpret using a compound microscope. Nearly all specimens have the lobes orientated differently, even on each side of the body. The lobes on the main illustration (Fig. 4) are orientated dorsoventrally; those on the enlargement on the left show their orientation on the holotype; those in the middle show how we suspect the lobes curve around the anal opening and illustrate their three-dimensionality, whereas those on the right enlargement show how they might appear in ventral view. The microtubular ducts each seem to be partially divided longitudinally, but lack the projecting apex found on immature instars. The rectangular plate apparently is not situated on the dorsal surface, but is in a separate cavity that opens onto the dorsum just anterior of the triangular plate.

Second-instar female (Fig. 5) (described from 3 specimens). *Mounted material*: Anal cleft absent. Total body length 1.0 (0.9–1.0) mm; width 0.5 mm. Derm with lightly sclerotized nodules over dorsum and margin of venter (indicated in Fig. 5, on head).

Dorsum: Enlarged setae slightly curved, of one variable size, mediolateral and submedial setae slightly shorter than those near margin, arranged in 2 pairs of longitudinal lines (excluding those near margin), one pair submedial and one pair mediolateral, extra setae present on anterior abdominal segments and on thorax; longest enlarged seta 59 (58–60) μm. Microtubular ducts as on adult female except with dermal orifice bifurcate, associated with longitudinal lines of enlarged setae. Anal lobes triangular when orientated with dorsal surface facing up, but in life probably with each lobe lying vertically, with inner margin lying ventrally; sclerotized, with a series of conspicuous teeth on inner margin; each lobe with a total of 7 setae, including anterior suranal and elongate posterior suranal seta, plus 2 or 3 microtubular ducts; lobe length 71 (55–80) μm; lobe width 59 (58–60) μm. Medial plate triangular, sclerotized, with nodulose surface, without microtubular ducts. Sclerotized rectangular plate anterior to medial plate absent.

Margin: Without distinct marginal row of setae. Anal ring not situated in invaginated cavity between dorsal and ventral surface; anal tube absent; with single row of anal ring pores and with 3 pairs of anal ring setae; width 38 (38–39) μm; longest anal-ring seta 80 (75–84) μm; ratio of length of longest anal-ring seta to width of anal ring 2.1 (2.0–2.1):1.

Venter: Multilocular sessile pores normally with 5 loculi, rarely 3 or 4; arranged in 2 longitudinal lines on each side of body, each line comprised of 1 or 2 pores on each segment; multilocular sessile pores also present near spiracles and near legs; spiracular multilocular sessile pore bands absent. Cruciform pores more or less forming a line laterally between spiracles. Microtubular ducts present near body margin. Ventral setae arranged segmentally, slightly enlarged towards posterior end; anterior suranal seta enlarged, 24 (23–25) μm long; posterior suranal seta also enlarged. Width of each eyespot 16 (15–18) μm. Width of each spiracular peritreme 12 μm.

Legs: Measurements of hind leg: trochanter + femur 95 μm; tibia 47 (43–49) μm; tarsus 76 (75–78) μm; ratio of tibia to tarsus 0.6 : 1; ratio of trochanter + femur to tibia 2.0 (1.9–2.2):1.

Antennae: Length 153 (148–160) μm.

Labium: Length 96 (87–105) μm. Chaetotaxy on legs and labium as for adult female.

First-instar nymph (sex not determined) (Fig. 6) (described from 2 fully formed first-instar nymphs and 2 embryos). *Mounted material*: Anal cleft absent. Total body length 0.6 (0.5–0.7) mm; width 0.3 (0.2–0.4) mm. Derm with lightly sclerotized nodules over dorsum and margin of venter (shown in Fig. 6 on dorsum of segment VII).

Dorsum: Enlarged setae slightly curved, variable in size, with mediolateral and submedial setae on abdominal segments 1–7 noticeably shorter than marginal setae, arranged in 2 pairs of longitudinal lines (excluding marginal ones), one pair submedial and one pair medial, with one seta in each mediolateral and submedial position on each abdominal and thoracic segment, without extra setae; longest enlarged seta 40 (35–42) μm long. Microtubular ducts as on adult female except with bifurcate dermal orifice; ducts associated with mediolateral longitudinal lines of enlarged setae. Anal lobes triangular, each with a series of conspicuous teeth on inner margin; with a total of 6 setae on each lobe, including anterior suranal and elongate posterior suranal setae; lobes without microtubular ducts; lobe length 44 (42–45) μm; lobe width 40 μm. Medial plate quadrate,

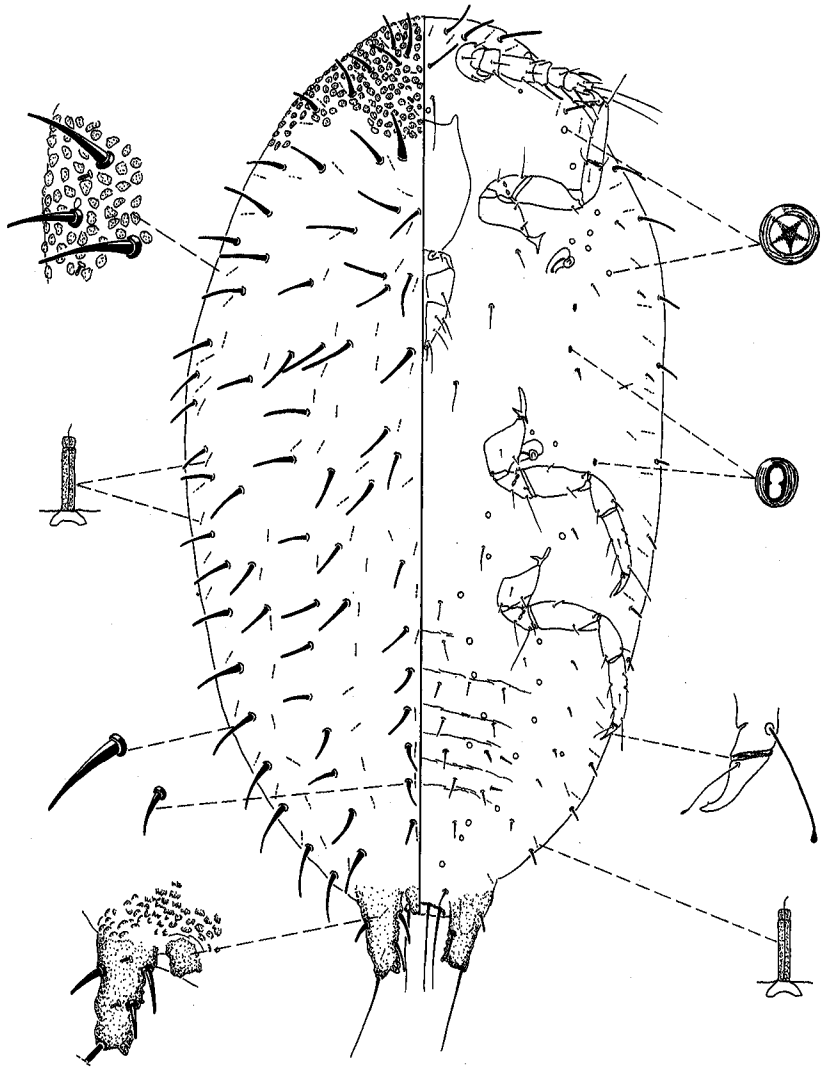

Fig. 5. *Icelococcus lithreae,* second-instar female.

sclerotized, with several teeth posteriorly, without a microtubular duct. Sclerotized rectangular plate anterior to medial plate absent.

Margin: Without distinct marginal row of setae. Anal ring not situated in invaginated cavity between dorsal and ventral surfaces; with a single row of anal ring pores and with 3 pairs of anal ring setae; anal tube absent; width of anal ring 24 (25–29) μm; longest anal-ring seta 48 (42–50) μm; ratio of length of longest anal-ring seta to width of anal ring 1.8 (1.6–1.9):1.

Venter: Multilocular sessile pores each normally with 3 loculi, rarely 5; arranged in one longitudinal line on each side of body (near base of each mediolateral seta), with one pore on each side of each segment; also with one present near each spiracle, 2 present near margin of thorax and head, and one present between antennae. With one cruciform pore laterad to each spiracle. Microtubular ducts absent. Ventral setae arranged segmentally, not enlarged; both anterior and posterior suranal setae bristle-shaped, each anterior seta 25 (22–28) μm long. Width of each eyespot 13 (12–15) μm. Width of each spiracular peritreme 8 μm.

Legs: Measurements of hind leg: trochanter + femur 67 (56–78) μm; tibia 30 (20–36) μm; tarsus 52 (42–56) μm; ratio of tibia to tarsus 0.6 (0.5–0.7):1; ratio of trochanter + femur to tibia 2.2 (2.0–2.3):1.

Antennae: Length 114 (105–122) μm.

Labium: Length 75 (70–80) μm. Chaetotaxy on legs and labium as for adult female.

Note. The two embryos used in the above description were sufficiently well developed to allow measurements of the leg segments and to observe structural details to incorporate them in the data matrix. One additional embryo was also referred to when morphological characters were visible, but for the most part, they were not used in

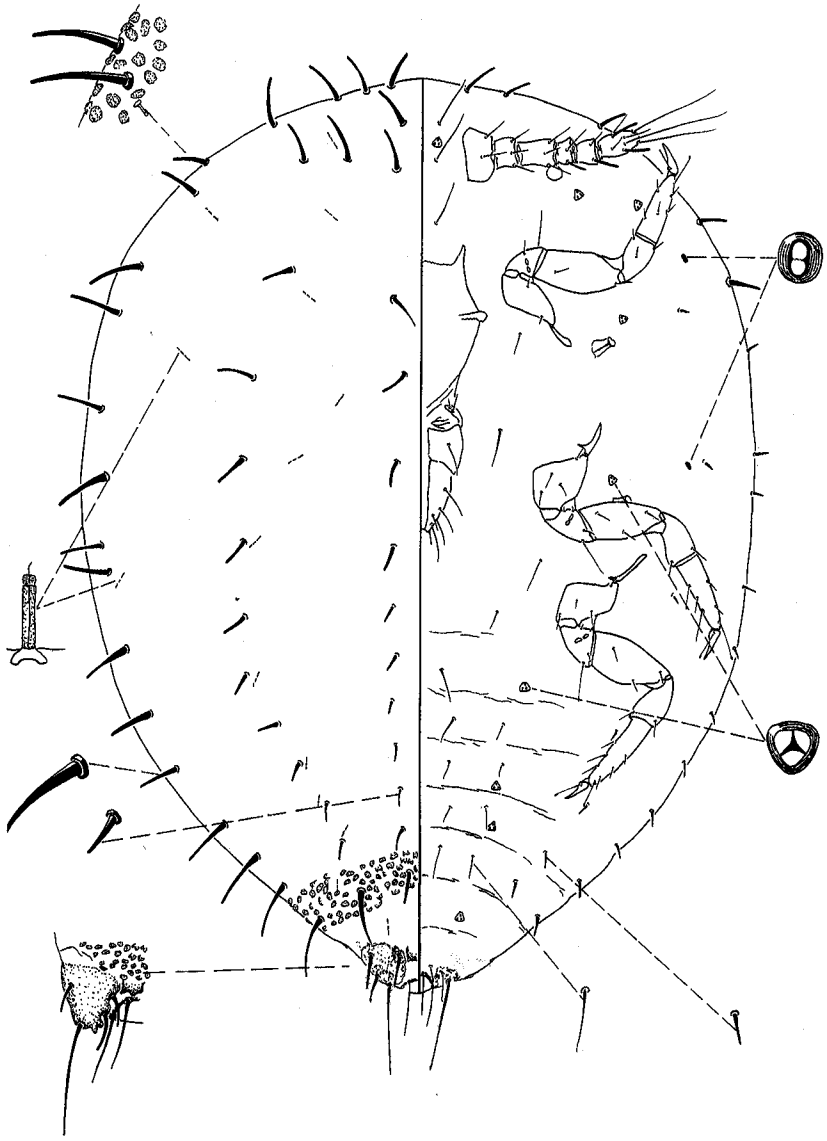

Fig. 6. *Icelococcus lithreae*, first-instar nymph.

the description. One of the mounted first-instar nymphs is in the process of moulting and it is evident that it is moulting into a second-instar male as it has macrotubular ducts scattered over the dorsum. This character is diagnostic of second-instar males (Miller *et al.*, 1992).

Remarks. Icelococcus lithreae closely resembles other species of the genus (see generic diagnosis above) with the adult female differing in the absence of translucent pores on the metacoxae, the structure of the microtubular ducts, which are sclerotized throughout, the position of the vulva and the presence of a sclerotized plate anterior of the anal lobes. However, the position of *I. lithreae* in the successively weighted cladogram (Fig. 7) requires that *I. lithreae* either be placed in a monotypic genus or that it be lumped in a genus containing *Chilechiton lynnae*, *Eriochiton* spp., *Icelococcus nothofagi* and *Neoeriochiton clareae*. Nevertheless, we have decided to include this species in *Icelococcus* until more taxa are known because we suspect that many more species will be discovered.

History. In 1986, Enrique Zuniga (Instituto de Investigaciones Agropecuarias, La Cruz, Chile) submitted a series of specimens for identification to the second author. Zuniga collected them in the forests of Parque Nacional La Campana, Olumé, primarily on *Lithraea caustica* (Anacardiaceae), but he also noted what he considered to be the same species on *Crinodendron patagua* (Elaeocarpaceae), *Luma chequen* and *Peumus boldus* (Monimiaceae). Because of the large amount of honeydew produced by this species,

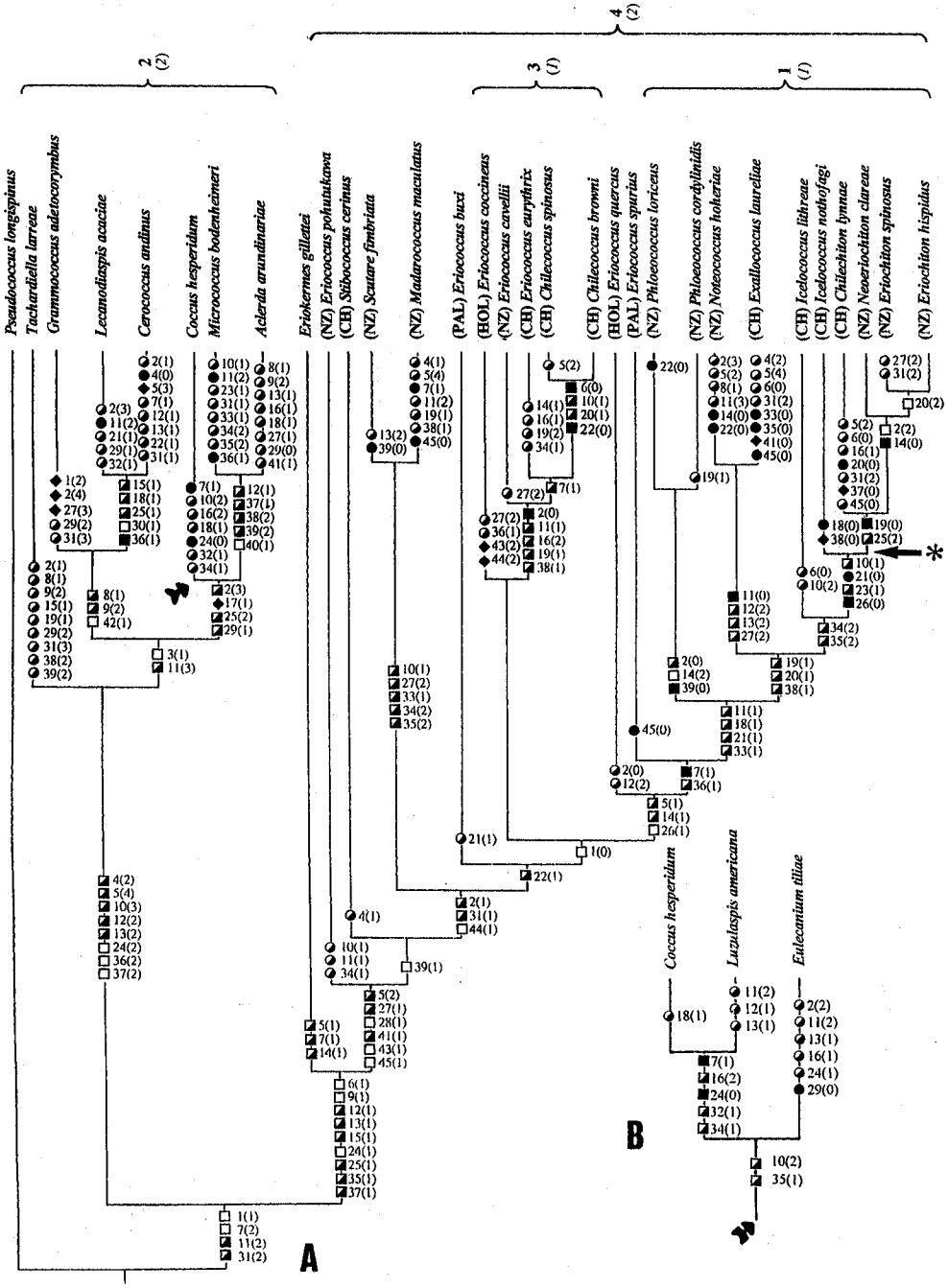

Fig. 7. A, Main cladogram produced from twelve equally parsimonious cladograms by successive weighting, using forty-five characters from the adult female, but with some character states taken from first-instar nymphs when characters not available on adult female; character states unordered and with *Pseudococcus longispinus* as outgroup. Length 208 steps, CI = 0.38, RI = 0.65. Note that the narrow black arrow with an asterisk (*) indicates the basal internode for the newly diagnosed Eriochitonini, and that squares refer to synapomorphic character states, circles to symplesiomorphic character states, black diamonds to autapomorphic character states, half-white circles and half-white squares refer to convergencies, and black circles and black squares to reversals. CH = Chile; HOL = Holarctic; NZ = New Zealand; PAL = Palaearctic. B, New structure for coccid branch when *Luzulaspis americana* and *Eulecanium tiliae* are added. This clade would replace the *C. hesperidum* branch at the node indicated by the thick black arrow. No other changes were introduced to the main cladogram by the addition of these two species (length 214 steps, CI = 0.37, RI = 0.68). The major clades discussed in the text are shown by the emboldened Roman figures and the Bremer support is shown by the italicised figures in brackets below the Roman figures.

approximately 60% of the foliage of the forest was covered with sooty mould. He was concerned that there would be significant damage to the forest and surmized that the species must be introduced. This would appear to be unlikely.

Etymology. Although similar to the host's generic name *Lithraea*, the species epithet *lithreae* is to be treated as a noun in apposition and a random combination of letters.

Results of the phylogenetic analysis

The main phylogenetic analysis produced twelve equally most parsimonious cladograms of 208 steps, with CI = 0.38, RI = 0.65. The twelve cladograms differ in slight rearrangements of the lineage containing *Aclerda arundinariae*, *Cerococcus andinus*, *Coccus hesperidum*, *Grammococcus adetocorymbus*, *Lecanodiaspis acaciae*, *Micrococcus bodenheimeri* and *Tachardiella larreae*, and in the association or lack of association of *Eriococcus buxi* with the clade composed of *Madarococcus maculatus* and *Scutare fimbriata*. Successive weighting resulted in a single most parsimonious cladogram (Fig. 7). This cladogram was not identical to any of the twelve cladograms but differed only in a small rearrangement of clade (ii) (see Fig. 7) (i.e. *Aclerda*, *Cerococcus*, *Coccus*, *Grammococcus*, *Lecanodiaspis*, *Micrococcus* and *Tachardia*). This cladogram will be used for further discussions of the relationships of the group. When a general heuristic analysis was run allowing all cladograms with one extra step, i.e. 209 steps, there were 490 cladograms produced and the strict consensus of these had four major clades containing clade 1 – *Chilechiton lynnae*, *Eriochiton spinosus*, *E. hispidus*, *Neoeriochiton clareae*, *Exallococcus laureliae*, *Icelococcus lithreae*, *I. nothofagi*, *Noteococcus hoheriae*, *Phloeococcus cordylinidis* and *P. loricae*; clade 2 – *Aclerda arundinariae*, *Cerococcus andinus*, *Coccus hesperidum*, *Grammococcus adetocorymbus*, *Lecanodiaspis acaciae*, *Micrococcus bodenheimeri* and *Tachardiella larreae*; clade 3 – *Chilecoccus browni*, *C. spinosus*, *Eriococcus eurythrix*, *E. coccineus* and *E. cavellii*; and clade 4 – all eriococcids, including those mentioned in clades 1 and 3 plus *Eriococcus buxi*, *E. pohutukawa*, *E. quercus*, *E. spurius*, *Madarococcus maculatus*, *Scutare fimbriata* and *Stibococcus cerinus* basal in the clade. *Eriokermes gillettei* was basal in the overall cladogram (Fig. 7). The Bremer support for the various clades is also shown in Fig. 7. Only clades 2 and 4 had Bremer support of 2, but clade 2 contains all of the non-eriococcid taxa, whereas clade 4 contains all Eriococcidae. Thus, although the support for these clades is not entirely satisfactory, this study does support the view that Eriococcidae and Coccidae are not closely related. A third decay step (211 steps) produced more than 32 000 cladograms but maintained clade 1 95% of the time, and the eriococcid clade, clade 4, 96% of the time.

We also experimented with different outgroup taxa to see what impact this might have on cladogram structure. When we deleted *Pseudococcus longispinus* from the analysis and used any or all of *Aclerda arundinariae*, *Cerococcus andinus*, *Coccus hesperidum*, *Grammococcus adetocorymbus*, *Lecanodiaspis andinus* or *Micrococcus bodenheimeri* as the outgroup, we obtained three equally parsimonious cladograms, with 195 steps, CI = 0.40, RI = 0.65. The three cladograms were essentially the same as Fig. 7, except that clade 2 was divided and there were minor differences in the positions of *Eriococcus coccineus* and *E. buxi*. The relationships within clade 1 remained the same.

To more carefully examine the relationships of Eriochitonini and its relatives, we ran additional analyses of clade 1. First, we included all of the eriococcids and used any or all of *Chilecoccus browni*, *C. spinosus*, *Eriococcus buxi*, *E. cavellii*, *E. coccineus*, *E. eurythrix*, *E. pohutukawa*, *E. quercus*, *E. spurius*, *Madarococcus maculatus* or *Scutare fimbriata* as outgroup taxa. In each case, there was a single most parsimonious cladogram of 111 steps (CI = 0.43, RI = 0.62). Although there was some variation in the relative positions of *Chilecoccus browni*, *C. spinosus*, *Eriococcus buxi*, *E. cavellii*, *E. coccineus*, *E. eurythrix*, *E. pohutukawa*, *E. quercus*, *E. spurius*, *Madarococcus maculatus* and *Scutare fimbriata*, the structure of clade 1 remained constant and was identical to that shown in Fig. 7. This clade maintained itself through one decay step in the strict consensus and was present after four steps in the majority rule consensus at a level of 92% or higher. In the second series of analyses, we included only the taxa in clade 1 and tested each of the remaining eriococcid taxa as outgroup taxa. There were eight different topologies; four of which were duplicated once, including the structure shown in Fig. 7. These cladograms had on average of 58 steps (CI = 0.66, RI = 0.62). The only uniformity in the resulting cladograms was that, in all but two, the lineage composed of *Chilechiton lynnae*, *Eriochiton spinosus*, *E. hispidus* and *Neoeriochiton clareae* had the same structure as in Fig. 7 and these were normally apical, whereas the two species of *Phloeococcus* formed a clade in all but one analysis, with them usually basal. The remaining taxa showed little uniformity in their relative positions.

Because the main set of analyses above contained only one member of Coccidae (*Coccus hesperidum* Linnaeus: subfamily Coccinae) and, to consider more carefully the relationship between Coccidae and Eriococcidae, another phylogenetic analysis was undertaken with the inclusion of two additional coccid subfamilies, Eriopeltinae (*Luzulaspis americana* Koteja & Howell) and Eulecaniinae (*Eulecanium tiliae* (Linnaeus)). The same characters and character states and the same analyses as described above were used. The initial analysis produced thirty-three equally parsimonious cladograms, with a length of 214 steps, CI = 0.37 and RI = 0.68. The strict consensus was similar to that in Fig. 7, with the coccid clade (*Coccus*, *Eulecanium* and *Luzulaspis*) as part of what was clade 2 in the first main analysis. The successively weighted cladogram maintained this structure, with Coccidae unrelated to Eriococcidae. When a general heuristic analysis was run allowing all cladograms with one extra step (i.e. 215 steps), there were

1217 cladograms and the strict consensus still had the coccid clade within the larger clade 2. With a second decay (allowing 216 steps), there were 22 570 cladograms and the coccid clade no longer appeared in the strict consensus but was listed as occurring in 100% of the cladograms in the 80% consensus. It is considered that the addition of further coccid taxa would have not changed these conclusions.

Discussion

The primary purpose of the phylogenetic analysis was to study the relationships of the Chilean and New Zealand eriococcid genera covered in this study, to review the boundaries of tribe Eriochitonini and to look at the relationship between the New Zealand and Chilean eriococcids and family Coccidae, to which they show a considerable resemblance.

The results of the current study demonstrated a very close relationship between some of the eriococcid genera from New Zealand and Chile. One of the best-supported clades, clade 2 above, included only Chilean and New Zealand genera (*Chilechiton*, *Eriochiton*, *Exallococcus*, *Icelococcus*, *Neoeriochiton*, *Noteococcus* and *Phloeococcus*, see Fig. 7). This clade was recovered on all the cladograms found in this study, including all those from the many outgroup analyses. This clade was sufficiently well defined to survive one decay step using a strict consensus analysis and three or four decay steps at a level above 90% in a majority-rule consensus. The four character states that diagnose clade 1 are: anal opening invaginated (ch. 18, state 1), presence of a sclerotized plate anterior to anal lobes (ch. 21, state 1), absence of macrotubular ducts (ch. 33, state 1) and the presence of three trochanter setae (ch. 11, state 1). Unfortunately, none of these is perfect as there is a reversal to no invagination in the anal opening in *Icelococcus nothofagi* and an independently developed invaginated anal ring in *Aclerda arundinariae*, *Cerococcus andinus*, *Coccus hesperidum* and *Lecanodiaspis acaciae*; the sclerotized plate is lost in the clade comprising *Chilechiton lynnae*, *Eriochiton hispidus*, *E. spinosus* and *Neoeriochiton clareae* and independently developed in *Eriococcus buxi* and *Lecanodiaspis acaciae*; macrotubular ducts are present in *Exallococcus laureliae* and independently lost in *Madarococcus maculatus* and *Scutare fimbriata*; and the number of trochanter setae has increased to four (ch. 11, state 0) on *N. hoheriae* and *E. laureliae* and there is convergence with other taxa outside this clade. We therefore considered it would be premature to redefine this clade as Eriochitonini, although this might be an option following further study.

Discovery of close faunal connections between the eriococcids of Chile and New Zealand is not new. Hoy (1962) suggested this possibility in his monograph on Eriococcidae of New Zealand, but his hypothesis did not accrue significant evidence until the work by Miller & González (1975). They listed seven character states shared by the eriococcids of Chile and New Zealand that do not occur in the faunas of either northern South America or North America. The discovery of *Chilechiton lynnae* provides further evidence documenting the similarities of these faunas. In contrast, the European, North American, South American and New Zealand species of *Eriococcus* are interspersed throughout the eriococcid clade and it seems unlikely that the geographical relationships that they imply would be maintained with the addition of more taxa.

Eriochitonini, as defined by Hodgson (1994) and enlarged by Henderson & Hodgson (1995) and Hodgson & Henderson (1996), included species in the genera *Eriochiton* and *Neoeriochiton*. The adult females of Eriochitonini were characterized by Hodgson (1994) as having 'a distinct anal cleft, an anus which lacks an anal tube, a pair of sclerotized, triangular, platelike anal lobes at the anterior end of the anal cleft and a small triangular plate between them anteriorly, and with the opening of the vulva between the 5th and 6th visible segments.' This definition also applies to *Chilechiton lynnae*. The clade which includes *C. lynnae*, *Eriochiton spinosus*, *E. hispidus* and *Neoeriochiton clareae* is defined in our analysis by the presence of setose anterior suranal setae (ch. 19, state 0), which is synapomorphic for this group alone), and the presence of platelike anal lobes (ch. 25, state 2), a character only showing convergence with non-eriococcid taxa. The occurrence of the South American species *Chilechiton lynnae* within Eriochitonini clade is strong support for the suggestion of a close connection between the two biotas in the past.

Seven species currently placed in *Eriococcus* were included in the study, including two European, two North American, one South American and two from New Zealand. Essentially, the members of this genus are scattered through the basal areas of the eriococcid clade and do not form a group and therefore the genus is polyphyletic according to out results. This finding requires further analysis using a larger sample of eriococcid taxa, including a long series of species currently placed in *Eriococcus*. However, it is evident that this genus is much more diverse than the current classification suggests.

The results of this study also indicated that the suite of eriococcid taxa examined form a monophyletic group that survives two steps in the decay analysis using a strict consensus and three steps using a majority consensus at 90% or higher. This differs from the conclusions of Cox & Williams (1987), Miller & Hodgson (1997) and Miller & Williams (1995), who treated the 'group' as paraphyletic. However, even in the current study, the characters that define Eriococcidae lineage are weak at best. Clearly, more research is needed in this area.

Miller & González (1975) noted that several of the Chilean eriococcid genera were surprisingly coccidlike in appearance and Hodgson (1994) and Hodgson & Henderson (1996) discussed similar findings for Eriochitonini in New Zealand. Miller & González (1975) were so impressed with the similarity that they suggested that the coccidlike eriococcids of Chile might be intermediate species and that Coccidae and Eriococcidae might be closely related. However, as with previous similar analyses mentioned in

the Introduction, we also found these two families were only distantly related. Other families, such as Aclerdidae, Micrococcidae, Kerriidae, Cerococcidae, Lecanodiaspididae and Asterolecaniidae, were more closely related to Coccidae than were Eriococcidae. Similar results have been presented by Foldi (1997), Miller & Miller (1993b) and Miller & Kosztarab (1979), but these latter authors did not examine Eriochitonini and its relatives.

The relationship of *Chilechiton lynnae* with *Eriochiton hispidus*, *E. spinosus* and *Neoeriochiton clareae* suggests two possible generic organizations. One would place all four species in a single genus called *Eriochiton*, but this would not recognize the distinctive features of *Neoeriochiton clareae* as described by Hodgson (1994). With the small number of taxa known from this group, we implemented a second alternative and place the new species in a separate monotypic genus, *Chilechiton*. The generic organization of *Icelococcus* species is also problematic. Placement of *Icelococcus lithreae* into a second monotypic genus is the most obvious approach for describing this interesting new species. *I. lithreae* and *I. nothofagi* generally are paraphyletic or more rarely polyphyletic in our analyses, but with such a paucity of known South American taxa, we have decided to place *lithreae* in *Icelococcus* until more species are discovered. We recognize the fact that these are somewhat arbitrary decisions but will wait for the discovery of more species before making more changes to the classification.

In conclusion, the cladogram presented here (Fig. 7) is not as well supported as we might have liked, but it does give reasonable answers to questions about the possible relationships of the New Zealand and Chilean eriococcids, the limits of Eriochitonini and the relationships of Coccidae and Eriococcidae.

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Appendix 1. Characters and character states.

Adult female (leg characters of first-instar nymphs used when legs absent from adult female)

1. *Number of setae on scape*: (0) 4; (1) 3 or less; (2) absent.
2. *Number setae on subterminal antennal segment*: (0) 4; (1) 3; (2) 2; (3) 1 or 0; (4) absent.
3. *Distribution of inter-antennal setae*: (0) in elongate group between antennae; (1) more or less in a transverse line.
4. *Number of labial segments*: (0) 3; (1) 2; (2) 1.
5. *Number of setae on basal labial segment*: (0) 3; (1) 2; (2) 1; (3) 0; (4) basal segment absent.
6. *Frontal lobes/antennal tubercles*: (0) absent; (1) present.
7. *Number of antennal pores*: (0) 3; (1) 2 or 1; (2) absent.
8. *Legs*: (0) well developed; (1) reduced or absent.
9. *Relative lengths of tibia and tarsus*: (0) tarsus < tibia; (1) tarsus > tibia; (2) legs absent.
10. *Size of translucent pores*: (0) small/minute; (1) large; (2) absent; (3) legs absent.
11. *Number of trochanter setae (excluding those next to coxa)*: (0) 4+; (1) 3; (2) 2; (3) 1.
12. *Number of femoral setae*: (0) > 10; (1) 5–10; (2) < 5.
13. *Number of tibial setae*: (0) > 10; (1) 4–9; (2) < 4.
14. *Number of setae on front tibia*: (0) number similar to hind tibia; (1) with one more on hind tibia than on front tibia; (2) more on front tibia than on hind tibia.
15. *Claw denticle*: (0) absent; (1) present.
16. *Claw digitules*: (0) both fine; (1) dissimilar; (2) both broad.
17. *Tarsal campaniform pore*: (0) present; (1) absent.
18. *Anal opening*: (0) not invaginated; (1) invaginated.
19. *Shape of anterior suranal setae*: (0) setose; (1) spinose; (2) spatulate.
20. *Shape of posterior suranal setae (ventral anal lobe seta)*: (0) setose; (1) spinose; (2) spatulate.
21. *Sclerotized plate anterior to anal plates*: (0) absent; (1) present.
22. *Median triangular plate between lateral lobes*: (0) absent; (1) present.
23. *Position of vulva*: (0) between VII and VIII; (1) between VI and VII.
24. *Number of pairs of anal ring setae*: (0) 3; (1) 4; (2) other.
25. *Anal lobes*: (0) absent or small; (1) protruding; (2) as anal plate.
26. *Anal lobes serrated along inner margin*: (0) no; (1) yes.
27. *Shape of dorsal setal*: (0) setose; (1) spinose; (2) both; (3) absent.
28. *Shape of basal sockets of marginal setae*: (0) broad; (1) narrow.
29. *Marginal setal shape*: (0) spinose; (1) setose; (2) absent.
30. *Cribriform*: (0) absent; (1) present.
31. *Marginal setae*: (0) cerarii; (1) undifferentiated; (2) differentiated; (3) absent.
32. *Stigmatic setae*: (0) undifferentiated; (1) differentiated.
33. *Macrotubular ducts*: (0) present; (1) absent.
34. *Inner ductule of macrotubular ducts*: (0) fine; (1) broad; (2) ducts absent.
35. *Cup-shaped invagination on macroducts*: (0) absent; (1) present; (2) without ducts.
36. *Cruciform pores*: (0) absent; (1) present and convex; (2) present and concave.
37. *Multilocular sessile pores in spiracular bands*: (0) absent; (1) present, diffuse; (2) present, in distinct bands.
38. *Multilocular sessile pores on abdomen*: (0) across segments; (1) in a line mediolaterally; (2) absent.
39. *Number of loculi in multilocular sessile pores*: (0) > 5 loculi; (1) 5 loculi; (2) pores absent.
40. *Multilocular sessile pores in atrium of spiracle*: (0) absent; (1) present.
41. *Simple pores*: (0) present; (1) absent.
42. *Eight-shaped pores*: (0) absent; (1) present.
43. *Microtubular ducts, shape*: (0) absent; (1) long; (2) short.
44. *Microtubular ducts on dorsum*: (0) absent; (1) single apex; (2) double apex.
45. *Microtubular ducts on venter*: (0) absent; (1) present.

Appendix 2. Character matrix.

	Character number								
		1		2		3		4	
	12345	67890	12345	67890	12345	67890	12345	67890	12345
Pseudococcus longispinus	00000	00000	00000	00000	00000	00000	00000	00000	00000
Aclerda arundinariae	13124	02123	31100	11100	00022	01000	20001	21221	10000
Chilecoccus browni	00001	01011	11101	20011	00011	01100	10001	01110	10111
Chilechiton lynnae	01002	01011	11111	10100	01112	01100	20122	10110	10110
Chilecoccus spinosus	00002	01011	11101	20011	00011	01100	10001	01110	10111
Cerococcus andinus	11103	01123	31101	00100	01021	00011	10001	12000	01000
Coccus hesperidum	13124	01002	32200	21100	00002	00010	21011	22000	00000
Eriochiton hispidus	02001	11011	11101	00102	01112	01100	10122	11110	10111
Eriochiton spinosus	02001	11011	11101	00102	01112	02100	20122	11110	10111
Eriococcus buxi	11002	12010	21101	00000	11011	01100	10001	01010	10111
Eriococcus cavellii	00001	12010	11101	20010	01011	02100	20001	01110	10111
Eriococcus coccineus	01001	12010	21101	00000	01011	02100	20001	11010	10221
Eriococcus quercus	00001	12000	22111	00000	01011	11100	10001	01010	10111
Eriococcus eurythrix	00001	11010	11111	10020	01011	01100	20011	01110	01111
Eriococcus pohutukawa	00002	12011	11101	00000	00011	01100	20001	01000	10101
Eriococcus spurius	01001	11010	21111	00000	01011	11100	10001	11010	10110
Eriokermes gillettei	10001	11010	21111	00000	00011	00100	20001	01000	00000
Exallococcus laureliae	01024	01011	22211	00111	11011	12100	20000	11110	00110
Grammococcus adetocorymbus	24124	02123	32200	00000	00020	03020	300–1	22000	01000
Icelococcus lithreae	01001	01012	11111	00111	11011	11100	10122	11110	10111
Icelococcus nothofagi	01001	11011	11111	00011	01111	11100	10122	11010	10111
Lecanodiaspis acaciae	13124	02123	22201	001–0	10021	00011	21001	12000	01000
Madarococcus maculatus	11014	11011	11101	00020	0–011	02100	10122	01110	10110
Micrococcus bodenheimeri	13124	02001	21200	01000	00122	00010	10122	11221	00000
Neoeriochiton clareae	02001	11011	11101	00101	01112	01100	10122	11110	10111
Noteococcus hoheriae	03002	11110	32201	00111	10–11	121–0	101––	11110	10111
Phloeococcus cordylinidis	00001	11010	11121	00110	11011	11100	101––	11000	10111
Phloeococcus loriceus	00001	11010	11121	00100	10011	11100	101––	11000	10111
Scutare fimbriata	1–002	12011	2–201	00000	00011	02100	10122	01000	10111
Stibococcus cerinus	1–01–	––010	–1101	000–0	00011	01100	20001	01010	10101
Tachardiella larreae	11024	02123	22201	0001–	–002–	00020	30001	22220	00000
Eulecanium tiliae	12124	02002	22100	11100	00012	00000	21011	22000	00000
Luzulaspis americana	13124	01002	21100	21100	00002	00010	21011	22000	00000