The morphology of lac insects (Hemiptera: Coccoidea: Kerriidae)

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Abstract: Lac insects constitute a family, the Kerriidae, of morphologically peculiar scale insects that produce resinous secretions that mostly form a hard scale cover or test. Identification to species level is based on membranous, globose adult females that are difficult to slide-mount and have a complex morphology that is unfamiliar even to most coccidologists. Characteristics important to species recognition are poorly understood in most genera, and the species diversity of lac insects probably has been underestimated. Here we present an overview of the cuticular morphology of the Kerriidae, with emphasis on features most important for species identification, such as the anal tubercle, brachial plate, dorsal spine and marginal and ventral duct clusters. We provide a detailed illustration of the young adult female of *Kerria lacca* (Kerr), the lac insect of commerce.

Key words: Kerriidae, lac insects, morphology, *Kerria lacca.*

Introduction

Approximately 90 species of lac insects (Hemiptera: Coccoidea: Kerriidae) have been described worldwide in nine genera (Ben-Dov, 2006), based on a classification that was established by the monographic work of Joseph C. Chamberlin (1923, 1925). The most widely known lac insect species, *Kerria lacca* (Kerr), is renowned for the commercial use of its secretion, or shellac, as a natural polymer (Varshney, 1970; Yao *et al*., 1989; Ben-Dov, 2006). Some other lac insect species are plant pests that can cause branch dieback or even plant death (e.g., Campbell *et al*., 1994; Pemberton, 2003). Although taxonomic studies in China (e.g., Wang, 1986; Zhang, 1992, 1993), India (e.g., Varshney, 1977, 1984) and South Africa (Munting, 1965, 1966) have furthered our knowledge of kerriid diversity, and recent research by Ireneo L. Lit, Jr (Lit & Gullan, 2001; Lit, 2002a,b) has increased our understanding of basic lac insect morphology, accurate identification to species level remains challenging for several reasons. First there is the technical difficulty of preparing good microscope slide-mounts that are essential for seeing some of the diagnostic cuticular features. Adult females have globular, membranous bodies and, unless correctly flattened dorsoventrally, it may be impossible to distinguish or count structures such as the number of microducts in marginal and ventral duct clusters. Second, there is an idiosyncratic nomenclature associated with the peculiar and complex morphology of adult female lac insects, and this can be a deterrent to using keys or taxonomic papers. Third, we have a very poor understanding of what constitutes a lac insect species. There are no molecular phylogenetic or population genetic studies of lac insects, not even for *K. lacca* and its relatives, and our recent taxonomic study of *Paratachardina* Balachowsky (Kondo & Gullan, 2007) has shown that the adult females of closely-related species can be extremely similar in their cuticular morphology. It is likely that there are many undescribed species of kerriids.

Here we review the morphological features of the adult female lac insects, provide the first detailed illustration of the young adult female of *K. lacca* (the type species of the type genus *Kerria* Targioni Tozzetti), and discuss cuticular structures of taxonomic importance in the identification of kerriid species.

Materials and methods

Young adult females of *K. lacca* were slide-mounted from dry material deposited at the BME (Bohart Museum of Entomology, University of California, Davis). The collection

information for these specimens is as follows: "*Tachardia lacca* grown in Ceylon from imported stock on *Albizzia* sp., Peradeniya, Ceylon, No. 8940, E.E. Green", 11 slides, 11 specimens, slide-mounted by T. Kondo and P.J. Gullan, 2007. The illustration of *K. lacca* is a generalization of several specimens and was prepared with the assistance of a camera lucida attached to an Olympus BX40 compound microscope. The terms used to describe lac insects follow those of Chamberlin (1923), Gill (1993) and Kondo & Gullan (2005, 2007). Some important structures are illustrated in Figure 1, and others are shown in Figure 2.

Results and discussion

Lac insect females have three instars, i.e., first (crawler stage), second, and adult. Males, if present, have five instars, i.e., first, second, prepupal, pupal and adult. Although the current classification of lac insect genera and species is based almost entirely on the cuticular morphology of the adult females, in the future other instars, especially first-instar nymphs, may become useful for identification. For a generalized drawing of a lac insect first-instar nymph, see Miller (1991); for a description of the first-instar nymph of *K. lacca* see Misra (1931); for the first- and second-instar nymphs of a *Paratachardina* species, see Kondo & Gullan (2007).

Lac insects are a morphologically distinctive group of scale insects characterized by adult females with the following features: (i) body generally covered in a resinous test; (ii) dorsal spine present (absent in only one species); (ii) brachial plates present; (iii) anal tubercle present and usually composed of a sclerotized supra-anal plate and usually a less sclerotized pre-anal plate; (iv) anal ring with 10 setae; (v) antennae with 1–7 segments; (vi) legs reduced or absent; (vii) anterior spiracles located on body margin or on dorsum, and much larger than posterior spiracles; (viii) canella (anterior spiracular furrow lined with pores) present or absent; (ix) ventral setae present, usually short and scarce; (x) marginal duct clusters present; (xi) ventral duct clusters usually present; (xii) spermatoid ducts present on both surfaces of body: on venter restricted generally to marginal and submarginal areas and most abundant within each marginal duct cluster, and on dorsum more-or-less widely distributed throughout, but usually with areas devoid of ducts, e.g., around dorsal spine, anal tubercle and brachial plates. Within a species, the body shape of the adult female can vary considerably (see Takahashi (1941) for illustration of this variation in *K. lacca*), depending on age and growth conditions.

The adult female resembles the second-instar female, but differs as follows (character states of second instar in parentheses if appropriate): (i) larger body size; (ii) with many more ducts and pores; (iii) larger brachial plates; (iv) well developed brachia (absent in the second instar); (v) almost always with a dorsal spine (absent or represented by a membranous lobe); and (vi) perivulvar pores present in some taxa (always absent). Besides their smaller size, first-instar nymphs are readily differentiated from subsequent instars by: (i) presence of one pair of very long setae on the anal tubercle, each about half length of body; (ii) well developed antennae with 6 segments; (iii) cursorial legs; and (iv) lack of brachial plates and brachia (Misra, 1931; Miller, 1991; Kondo & Gullan, 2007).

Adult female: the resinous test

Typically the lac test is composed of a hard resin, although the test is described as sticky in *Austrotachardiella sexcordata* Matile-Ferrero (Matile-Ferrero & Couturier, 1993). The tests of many lac insect taxa dissolve in alcohol, whereas tests of other taxa, such as *Paratachardina* species, do not dissolve (Varshney, 1984). The tendency for some tests to dissolve more

readily than others may have lead to the idea that some tests are gum-like and pliable, but there is no comparative study of lac insect tests, and the chemistry of very few tests have been studied. The test greatly varies in shape and color, and often the tests of crowded individuals fuse to form a single mass. The test of a single individual may be unlobed and rounded, or with 3–6 marginal lobes. The surface of the test may be smooth or with a series of longitudinal ridges, and often various bumps or elevations may be present. According to Green (1922), the shape of the insect body can be reflected in the shape of its test.

Lac tests vary from dull brown or dark, to various tones of red or orange, although species with greenish or yellowish colors also exist. Each test is usually of a single colour, but some species may have characteristic color patterns, e.g., *Paratachardina decorella* (Maskell).

Adult female: cuticular structure

Dorsum. The derm is always membranous, and without visible segmentation. Dorsal setae (*dset*) generally are short and scarce, but usually are present around the body margin and often there are a few around the dorsal spine and dorsal tubercle. One of the most distinctive features of lac insects is a pair of brachial plates (*brpl*), each often elevated on a membranous to sclerotized, tubular protrusion called a brachium (*br*) [see Lit (2002a) for a discussion of other terms used for this structure]. Characteristics of the brachium and brachial plate have been used extensively for distinguishing species within genera (e.g., Chamberlin, 1923; Varshney, 1977; Kondo & Gullan, 2007) and for separating some genera (Chamberlin, 1923; Zhang, 1992; Kondo & Gullan, 2005). Each brachial plate is heavily sclerotized, and depending on species, can vary in shape from round, triangular, quadrate to irregular in outline, and may be flat or have a shallow or deep crater, or an elevated protrusion. Each plate bears brachial pores, brachial plate setae and pseudospines, the number of which can be informative for separating some species of *Paratachardina* (Kondo & Gullan, 2007), although variation within a species can confound taxonomic utility. Brachial pores usually have 5 loculi and are similar in structure to spiracular pores and canellar pores. A pseudospine is a specialized type of multilocular pore that resembles a seta or spine when viewed from the side, but a pore with 5 (rarely 3, 4 or 6 loculi) when viewed from above (Chamberlin, 1923; Lit, 2002a,b). In the first-instar nymphs, the homologous structures are hollow spines located in the anterior spiracular cleft and in the pseudocerarii (Miller ,1991). The brachia either can be absent, very short (sessile) or very long. Typically, the base of each brachium is associated closely with one of the large anterior spiracles; secretions from the brachial plate are believed to keep the spiracular openings of the test from being sealed over by the resin of the test (Chamberlin, 1923).

The dorsum is characterised by the presence of another unique structure, the dorsal spine (*dspi*), which is absent only in *Tachardina albida* Cockerell (Chamberlin, 1923). This conical, hollow spine is located anterior to the anal tubercle, and its apex probably always has an opening that connects to an internal duct, called the dorsal spine duct. The duct length and structure varies greatly among species, but ducts usually are divided into two types: (i) the dendritic type is most common and is quite branched throughout its entire length, as in *Austrotachardiella colombiana* Kondo & Gullan (Fig. 1A) and *K. lacca* (Fig. 2); and (ii) the non-dendritic (= fibrous) type is only known in *Austrotachardia* Chamberlin and is unbranched throughout its length, either ending on a swollen or a branched apex as in *A. melaleucae* (Maskell) (Fig. 1B) (Lit, 2001a). The dorsal spine is often elevated on a

membranous tube, called the pedicel, that can be very short or absent, or very long and slender as in *Albotachardina* species. The function of the dorsal spine and its duct is unknown (see Lit, 2002a for discussion of previous hypotheses), but any hypothesis must be able to account for lack of development of the dorsal spine in first- and second-instar nymphs (the latter are collected rarely and probably short-lived).

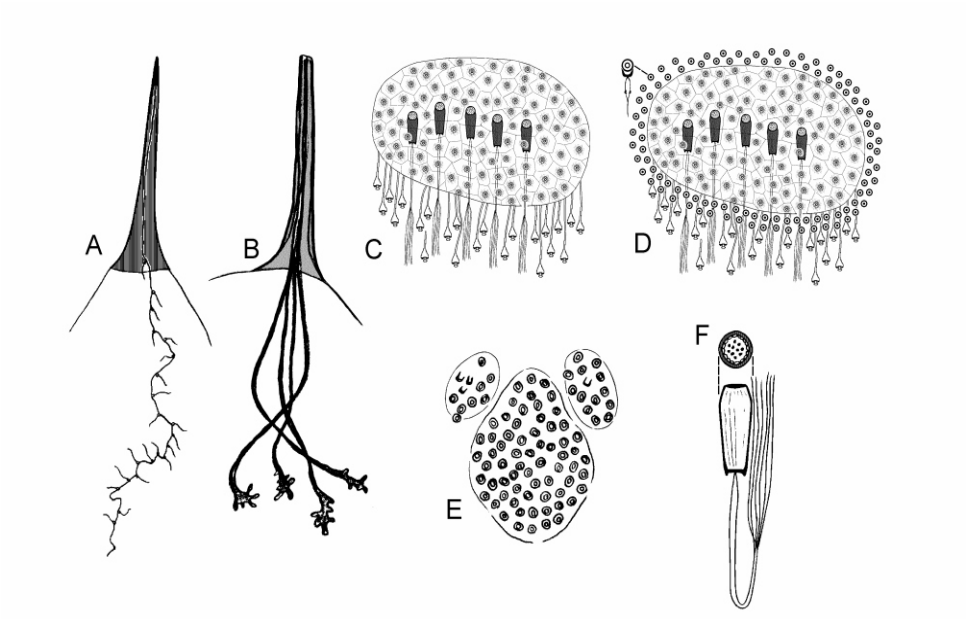

Figure 1. A, dorsal spine and dendritic spine duct of the adult female of *Austrotachardiella colombiana* Kondo & Gullan; B, dorsal spine and non-dendritic spine duct of the adult female of *Austrotachardia melaleucae* (Maskell); C, duplex type of marginal duct cluster as in *Tachardiella* species; D, triplex type of marginal duct cluster as in *Austrotachardiella* species; E, marginal duct cluster with two associated auxiliary clusters as in *Afrotachardina brachysetosa* (Chamberlin); F, typical macroduct of *Austrotachardiella* species.

The anal tubercle (at) is another characteristic feature of lac insects, although in some members of the Coccidae that have a thick waxy covering, such as *Ceroplastes* Gray, the area surrounding the anal plates can be highly sclerotized and of a tubular shape somewhat similar to that seen in the Kerriidae. In lac insects, the anal tubercle is the posterior sclerotized prolongation of the body that bears the pre-anal plate (*papl*) (in some groups), the supra-anal plate (*spanpl*), the anal fringe and the anal ring (Fig. 2). The anal fringe (*af*) is a series of ligulate lobes at the apex of the anal tubercle encircling the anal ring. The anal ring of kerriids may be divided into 4, 6 or more distinct sections or it can be entire (unsegmented) or show partial segmentation, and it always has 10 setae and usually an irregular row of pores. Some species of *Paratachardina* and *Tachardina* Cockerell have pygidial apodemes, which are variably sclerotized internal rods or processes that extend from the base of the supra-anal plate posteroventrally. Chamberlin (1923:158) incorrectly stated that these apodemes extended to "caudad of the dorsal spine". They probably function as rigid attachments for muscles that move the anal tubercle or its components.

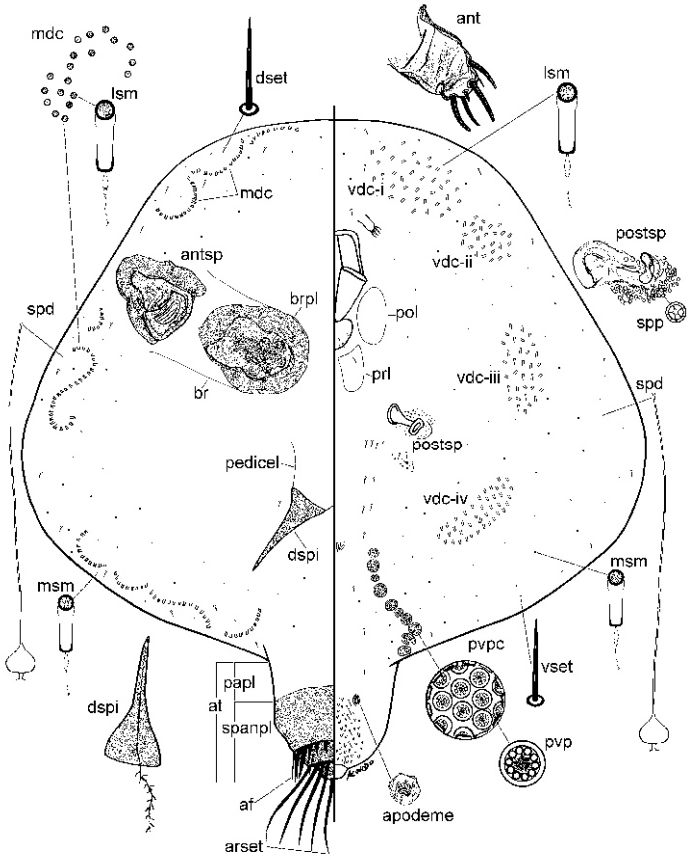

Figure 2. *Kerria lacca* (Kerr), young adult female (see text for abbreviations).

Microducts are either more or less scattered evenly throughout dorsum, or present only around the margins and submargins, and often there are fewer or absent around the anal tubercle, anterior spiracles, brachial plates and dorsal spine (Fig. 2). Microducts of the Kerriidae resemble the typical coccid ventral microduct, with a subcircular duct opening and short terminal gland. Spermatoid ducts (*spd*) (= spermatozooid ducts), which are unique to lac insects, are long thread-like ducts with a greatly swollen area at the inner end distal from the duct opening (Fig. 2). These ducts may occur singly on the derm or, in some genera, associated with the rim of microducts, and may contribute to the resin of the lac test. For a discussion of the naming of this duct, see Kondo & Gullan (2007).

The Margin. Unlike most other scale insects, the margins of lac insects are poorly defined and, in many species, it is hard to differentiate the dorsum from the venter after the adult female becomes mature and fully expanded (e.g., *K. lacca*). However, it is possible to locate the marginal areas by the presence of short setae or by the distribution of marginal duct clusters (*mdc*). The presence of mdcs is another distinctive characteristic of lac insects. Marginal duct clusters are subcircular to irregular clusters of microducts and/or macroducts and/or spermatoid ducts present around the body margin, usually on the venter, but

sometimes apparently on the dorsum (e.g., *K. lacca*). In *Afrotachardina* Chamberlin, mdcs have two closely associated auxiliary clusters of microducts (Fig. 1E). The typical microducts of most lac insects can be characterised arbitrarily as small-sized, medium-sized (*msm*) or large-sized (*lsm*) (Fig. 2). The structure of the different size classes of microducts generally are the same, however, in the New World genera *Austrotachardiella* Chamberlin and *Tachardiella* Cockerell, there are large-sized ducts, called macroducts (Kondo & Gullan, 2005; 2007), of a different structure to the smaller microducts. Macroducts have a cylindrical shape with a long and slender tail that splits near its end (Fig. 1F). The presence or absence, sizes, and combination of microducts, macroducts and spermatoid ducts in the mdcs can be useful features for identification at both the genus and species level. For example, the number of macroducts per marginal duct cluster is useful in separating species of *Austrotachardiella* and *Tachardiella* (Chamberlin, 1923; Kondo & Gullan, 2005). Chamberlin (1923) describes a series of types of marginal duct clusters. His simplex mdc consists of ducts of one size and structure, as in *K. lacca* (Fig. 2), his duplex mdc contains ducts of two types or sizes but with many variants of duct structure, whereas the triplex type of mdc has three kinds of ducts. In *Tachardiella*, duplex mdcs are composed of macroducts and spermatoid ducts only (Fig. 1C), whereas *Austrotachardiella* species have triplex mdcs composed of macroducts, spermatoid ducts and an outer narrow band of microducts (Fig. 1D). Chamberlin's classification into simplex, duplex and triplex mdcs fails to consider the homologies of duct types. For example, the name duplex mdc would be applied to an mdc with large central and small outer microducts, as well as to a mdc composed of macroducts and spermatoid ducts. Furthermore, Chamberlin (1923) confusingly refers to the central larger ducts of any type of mdc as "nuclear ducts", and to all other ducts in a cluster as "duplex ducts" (meaning secondary ducts), regardless of structure. The nature and function(s) of secretions from mdcs are unknown, but the secretions must contribute to the lac test.

The Venter. The derm is membranous, with segmentation sometimes visible on medial areas of the thorax and abdomen. Microtrichia are often present in segmental transverse rows in these areas, and usually a few setae (*vset*) are present on each of these segments. The antennae (*ant*) are always present and have 1–7 segments, although the segmentation is often poorly defined. Antennal position may vary from slightly anterolateral to the mouthparts, to near the body margin lateral to the mouthparts (as in *Paratachardina*), or displaced onto the dorsal surface of the head. The mouthparts of lac insects have a labium of 1–2 segments and generally 5–6 pairs of labial setae (Koteja, 1974). In some taxa, there are one or two pairs of membranous, often slightly sclerotized lobes surrounding the mouthparts. The lobes posterior to the mouthparts are called the post-oral lobes (*pol*) (Chamberlin, 1923) and more anterior lobes, if present, are called the pre-oral lobes (*prl*) (Kondo & Gullan, 2007). In the Kerriidae, as in all neococcoid scale insects, there are two pairs of thoracic spiracles and no abdominal spiracles. The anterior spiracles (*antsp*) of the adult female may be located either marginally or on the dorsum and always are larger than the posterior spiracles (*postsp*), which are present typically on the venter (Fig. 2).

The multilocular pores present surrounding the spiracular peritreme are called spiracular pores (*spp*) (vignette Fig. 2). These pores mostly have 5 loculi and are similar in structure to canellar pores and brachial pores. The term canella (plural canellae) was coined by MacGillivray (1921) for the spiracular furrow of scale insects, but was adopted later (Chamberlin, 1923) for the linear group of multilocular pores [canellar pores (*canp*)] between the anterior spiracles and mouthparts, or between the anterior and posterior spiracles as in some *Tachardiella* species. Recently Kondo & Gullan (2007) expanded the definition to

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Multilocular pores found around the vulva are called perivulvar (= perivaginal) pores (*pvp*), and are found generally within perivulvar (= perivaginal) pore clusters (*pvpc*), although they may occur singly (as in *Tachardina* species). Perivulvar pore clusters can be absent entirely in some genera (e.g. *Austrotachardia* and *Paratachardina*), or range from 4 in *Tachardiella* and *Austrotachardiella* to 18–50 in *Kerria*. Microducts usually vary in size within a species (as described for the dorsum), but microducts scattered on the derm often are smaller than those in the marginal and ventral duct clusters. The ventral duct clusters (*vdc*) are subcircular to irregular-shaped clusters of microducts present submarginally or submedially around the ventral body, and often lie parallel to the marginal duct clusters. The number of pairs of vdcs and the number of microducts per cluster are useful for separating species of some genera, e.g. *Paratachardina* (Kondo & Gullan, 2007). Spermatoid ducts, similar to those on the dorsum, usually are present marginally and submarginally on the derm but are most abundant within each marginal duct cluster and often also within the ventral duct clusters, and generally are absent from medial areas of the venter.

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