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ARE THE ENLARGED DUCTS OF *ERIOCOCCUS* (HEMIPTERA: COCCOIDEA: ERIOCOCCIDAE) PLESIOMORPHIC?

ABSTRACT

ARE THE ENLARGED DUCTS OF *ERIOCOCCUS* (HEMIPTERA: COCCOIDEA: ERIOCOCCIDAE) PLESIOMORPHIC?

Borchsenius (1948) separated the genus *Eriococcus* Targioni-Tozzetti (Eriococcidae) from *Acanthococcus* Signoret and *Gossyparia* Signoret on the basis of the occurrence of enlarged ducts in the adult female of the type-species, *E. buxi* (Fonscolombe). Enlarged ducts are found also in another Palaearctic species, a Chilean eriococcid and several Australian species of *Eriococcus*. The enlarged ducts of *Eriococcus* are similar in appearance and distribution to the large oral rim ducts of *Ferrisia* Fullaway (Pseudococcidae) and the dorsal tubercle ducts of *Ceronema* Maskell and some species of *Pulvinaria* Targioni-Tozzetti (Coccidae). It is argued that the enlarged ducts in taxa from each of these three families are homologous and therefore may be plesiomorphic for the Eriococcidae. If so, the possession of enlarged ducts is not of itself sufficient to justify the separation of *Eriococcus* as defined by Borchsenius.

Key words: macrotubular ducts, microtubular ducts, Aclerdidae, Cerococcidae, Coccidae, Kermesidae, Lecanodiaspididae, Putoidae, *Acanthococcus aceris*, *Ceronema banksii*, *C. dryandrae*, *Eriococcus buxi*, *E. eucalypti*, *E. williamsi*, *Exallococcus laureliae*, *Ferrisia virgata*, *Greenisca*, *Kaweckia*, *Lagosinia strachani*, *Pulvinaria dodonaeae*, *Rhizococcus*, phylogeny, morphology, wax.

INTRODUCTION

Several scale insect families are defined on plesiomorphic characters. The Margarodidae are defined by symplesiomorphies: characters that occur in sister groups to the scale insects and are therefore not shared derived characters unique to the margarodids (Miller, 1984). As a result, the Margarodidae have thus far resisted rigorous testing of monophyly (Miller, 1984; Foldi, 1997). The Eriococcidae also are problematic. Cox & Williams (1988) argued that the Eriococcidae are primarily separated from other coccoid families by the absence of the characters that help define other families rather than by the possession of unique characters (autapomorphies) that define the Eriococcidae as a monophyletic group. For example, all of the characters used by Ferris (1957) and Hoy (1962) to define the Eriococcidae (anal lobes, well-developed antennae, well-developed legs, tubular ducts, sessile pores and anal ring) are found also in other scale insect families. It appears likely that the anal lobes of eriococcids are homologous with those

of coccids (Cox & Williams, 1988; Hodgson, 1995). The macrotubular ducts with cupped inner ends found in eriococcids are also common in the Aclerdidae, Cerococcidae, Lecanodiaspididae, Coccidae (Williams, 1985b; Cox & Williams, 1988), Kermesidae and Putoidae. Microtubular ducts are found in many coccoid taxa, including the Pseudococcidae, and their morphology often differs even among eriococcid taxa. The anal ring structure is common to many of the neococcoid families and quinquelocular and multilocular pores are shared with most scale insect families. If these structures are homologous among the Eriococcidae and the other scale insect families in which they occur, then either the structures are plesiomorphic for the eriococcids (occurred in a common ancestor of eriococcids and the other taxa in which they are found), or the Eriococcidae are not monophyletic.

A lack of morphological synapomorphies also is a problem in respect of some genera within the Eriococcidae. One feature which has been used for generic diagnosis is the presence of enlarged ducts in adult females of Eriococcus *sensu* Borchsenius (1948), although not all authors accept this delineation. The most important characters for separating *Eriococcus* Targioni-Tozzetti from *Acanthococcus* Signoret are the absence of enlarged ducts in *Acanthococcus* and the presence in *Acanthococcus* of two ventral setae on each anal lobe (one in *Eriococcus*) and two pairs of setae on the basal labial segment (one pair in *Eriococcus*) (Williams, 1985b). Williams (1985b) considered these characters insufficient to warrant separation of the two genera. More recently, however, Miller & Gimpel (1996) restricted *Eriococcus* to those species with enlarged ducts and assigned the remaining species to *Acanthococcus*. *Eriococcus* has precedence over *Acanthococcus* whenever the two names are held to denote a single taxon (Melville, 1982). *Eriococcus buxi* (Fonscolombe) has been designated the type species of *Eriococcus* and *Acanthococcus aceris* Signoret is the designated type species of *Acanthococcus* whenever the two genera are considered different taxa (Melville, 1982).

There are several implications of treating the presence of enlarged ducts as diagnostic for a genus. Firstly, both *Eriococcus* (with enlarged ducts) and *Acanthococcus* (no enlarged ducts) should be recognised. Secondly, not all eriococcid species with enlarged ducts, such as *Exallococcus laureliae* Miller and González, clearly fit into either of these two genera. Thirdly, *Eriococcus sensu lato* is the most speciose eriococcid genus and, until recently, this generic name has been used for most species worldwide; delineation of *Eriococcus* based on the presence of enlarged ducts would restrict the application of this name to just a few species.

Williams (1985b) advocated the use of *Eriococcus sensu lato*, synonymising

Eriococcus, *Gossyparia* Signoret, *Acanthococcus*, *Rhizococcus* Signoret, *Greenisca* Borchsenius and *Kaweckia* Koteja & Zak-Ogaza, "until the world fauna is better understood". For nomenclatural stability, it is important to determine whether the occurrence of enlarged ducts warrants the separation of *Eriococcus*. Here it is argued that the enlarged ducts of eriococcids are homologous to those of some pseudococcids and coccids and therefore their mere presence or absence cannot be used to justify a distinction between *Eriococcus* and *Acanthococcus*.

Morphology and distribution of enlarged ducts

1. **Eriococcidae**

In all eriococcids in which enlarged ducts are present, the enlarged ducts are cylindrical, sometimes longitudinally ridged, and about 35 to 45µm long (Fig. 1A-C) with a blunt inner end from which a fine inner ductule arises. The external rim of the duct is circular and sclerotised. In *E. buxi*, there are no setae near the rim but in *E. williamsi* Danzig (referred to as *E.* sp. near *buxi* in Williams, 1985b) and the Australian *E. eucalypti* species-group, the enlarged duct is sometimes surrounded by enlarged (broadly lanceolate) setae. The enlarged ducts of the *E. eucalypti* species-group produce very long glassy wax filaments. The rim of the enlarged ducts of *Exallococcus laureliae* has been described as similar to that of oral-rim ducts of some pseudococcids (Miller & González, 1975).

The distribution of enlarged ducts varies slightly among eriococcid taxa. *Eriococcus buxi* has one or two pairs of enlarged ducts submarginally on the dorsum of the head (Williams, 1985b), whereas the *E. eucalypti* species-group has up to six pairs submarginally on the posterior abdominal segments and, in some specimens, several on the head and thorax. Enlarged ducts are totally absent in some individuals of some populations of the *E. eucalypti* species-group. *Eriococcus williamsi* has up to 17 pairs of enlarged ducts submarginally around the entire dorsum with others sometimes also present near the midline of the dorsum (Williams, 1985b). The pattern in *Exallococcus laureliae* is similar to that in *E. williamsi* although there are about 23 pairs present submarginally (Miller & González, 1975). In those eriococcid species for which crawlers have been examined (*E. buxi*, the *E. eucalypti* species-group and *Exallococcus laureliae*), enlarged ducts are expressed only in adult females.

There is variation in the appearance of the enlarged ducts among eriococcid species. For example, the blunt inner end of the enlarged duct of *E. buxi* has a quinquelocular appearance and that of *E. eucalypti* sp. 1 is flower-shaped.

2. **Coccidae**

In adult females of *Ceronema banksiae* Maskell, the enlarged ducts are about 50µm long with a blunt inner end (Fig. 1D & E) with a fine ductule. They sometimes appear to be longitudinally ridged (Hodgson, 1994). The rim is sclerotised and has several setae and numerous tubular ducts associated with it. There are about 27 pairs of enlarged setae submarginally around the dorsum. The enlarged ducts of *Ceronema dryandrae* Fuller appear to produce long glassy wax filaments which are most noticeable in young adult females and later become incorporated in the waxy test of the mature adult female. About 5 pairs of enlarged ducts are present submarginally in crawlers of *C. banksiae*, although they are smaller (about 20µm long) than those of adult females and there are no setae or tubular ducts associated with the sclerotised rim (Fig. 1F).

The adult female of *Pulvinaria* sp. near *dodonaeae* has approximately the same number and distribution of enlarged ducts as *Ceronema*. Each enlarged duct is about 35µm long and the sclerotised rim has several setae but only two smaller ducts associated with it (Fig. 1G & H). The smaller ducts are very similar in appearance to the microtubular ducts of some eriococcids. The blunt inner end of the enlarged tubular ducts in *C. banksiae* and *P.* sp. near *dodonaeae* has the appearance of a figure-of-eight-shaped pore.

Enlarged ducts are present also in some other coccids, such as *Lagosinia strachani* (Cockerell), in which there are about five pairs submarginally on the head and one to three pairs posteriorly on the abdomen (Hodgson, 1994).

3. **Pseudococcidae**

Enlarged ducts are present in *Ferrisia* Fullaway (McKenzie, 1967; Williams, 1985a) and numerous other mealybug genera (McKenzie, 1967). In *Ferrisia virgata* (Cockerell), the enlarged ducts (Fig. 1I) are about 35µm long and sometimes appear to be longitudinally ridged. They have a blunt inner end which has a quinquelocular appearance and a fine inner ductule. The rim is sclerotised and has several associated setae. There are up to 40 or more pairs of enlarged ducts submarginally around the dorsum and others present medially or scattered elsewhere on the dorsum. The dorsum of *F. virgata* has numerous glassy waxen rods (McKenzie, 1967) and it appears from their number and distribution that they are produced by the enlarged ducts. Crawlers of *F. virgata* do not possess enlarged ducts.

DISCUSSION

The enlarged ducts of representatives of the Eriococcidae, Pseudococcidae and Coccidae are very similar in morphology. All are cylindrical, between 35

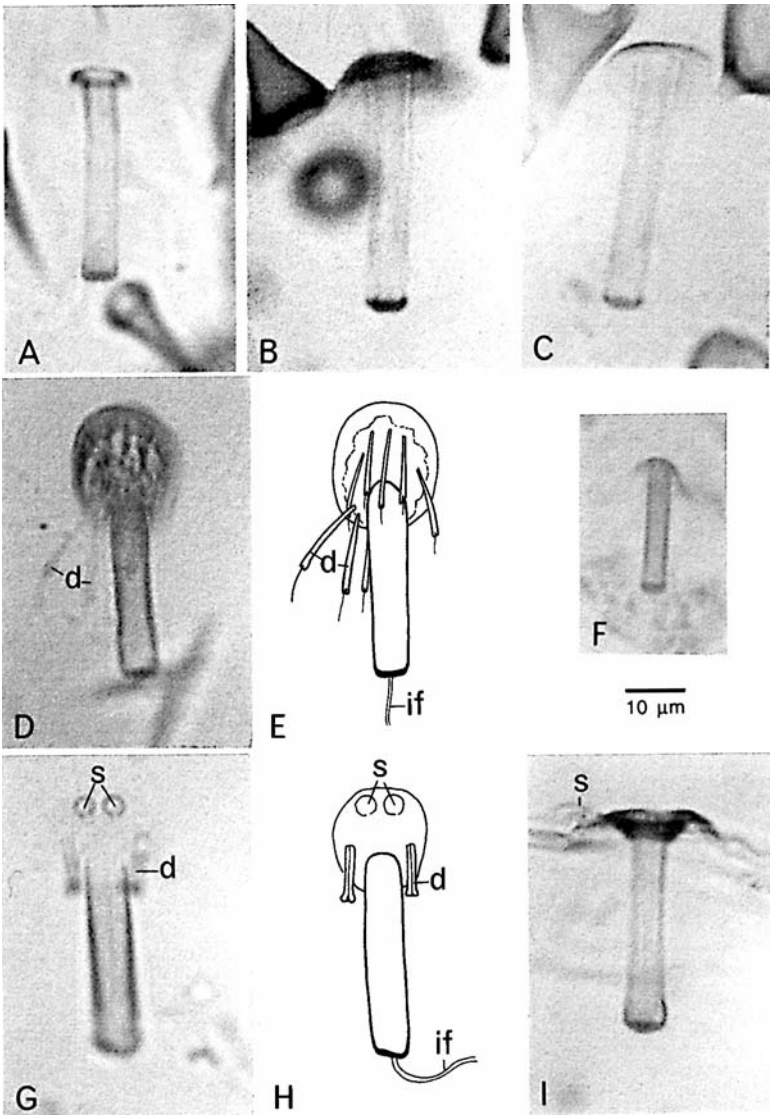

Figure 1. The enlarged duct of (A) *Eriococcus buxi* (Eriococcidae), (B) *Eriococcus eucalypti* group sp. 1 (Eriococcidae), (C) *Eriococcus eucalypti* group sp. 2 (Eriococcidae), (D) *Ceronema banksii* (Coccidae), (E) *Ceronema banksii* showing associated ducts (Coccidae), (F) *Ceronema banksii* (Coccidae) (crawler), (G) *Pulvinaria* sp. near *dodonaeae* (Coccidae), (H) *Pulvinaria* sp. near *dodonaeae* (Coccidae) showing associated ducts, (I) *Ferrisia virgata* (Pseudococcidae).
Associated ducts (d), inner filament (if) and setae associated with the rim (s) are indicated. The scale bar is the same for each figure.

and 50µm in length in the adult female, sometimes longitudinally ridged and have a blunt inner end with inner ductule. All have a sclerotised rim although the degree of sclerotisation varies among species. In at least some representatives of each of the three families, the enlarged ducts have associated setae. In addition, the appearance of the wax produced by the enlarged ducts appears to be similar in those species for which it has been observed.

The enlarged ducts display the same distributions in each of the three families. In *E. williamsi*, *Ex. laureliae*, *C. banksiae*, *P.* sp. near *dodonaeae* and *F. virgata*, enlarged ducts are located submarginally around the dorsum. In *E. williamsi*, *Ex. laureliae* and *F. virgata*, some enlarged ducts are also present medially on the dorsum. However, in *E. buxi* and the *E. eucalypti* species-group, *L. strachani* and crawlers of *C. banksiae*, the ducts are restricted to only a part of the distribution found in adult females of the other species.

It is unlikely that the morphology and distribution of enlarged ducts would be so similar in representatives of each of these families if they had evolved independently. The most parsimonious explanation is that a common ancestor of the Eriococcidae, Pseudococcidae and Coccidae possessed enlarged ducts with a sclerotised rim and associated setae and, possibly, ducts and/or pores. Under such a scenario, enlarged ducts are plesiomorphic for these families. If plesiomorphic, the presence of enlarged ducts in only a few representatives of each of the three families implies:

- that those taxa possessing enlarged ducts are basal within their respective families and the ducts have been lost in other more derived lineages, or
- that these taxa are not basal and the ducts have been lost many times, or
- that the expression of the ducts is plastic and they are not consistently expressed.

The first two possibilities cannot be addressed at present because there are no robust phylogenetic estimates available. The third alternative, however, is supported by the observation that, within populations of *E. eucalypti*, there is differential expression of enlarged ducts. Some adult females have enlarged ducts while others from the same host stem do not (Gullan & Cook, unpublished). Additionally, in those species discussed in this study, enlarged ducts of eriococcids and pseudococcids are expressed only in adult females whereas they are expressed in adult females and crawlers of *C. banksiae*. The

enlarged ducts in crawlers of *C. banksiae* are more similar to those of adult female eriococcids and *Ferrisia* than are those of adult females of *C. banksiae*. Perhaps the enlarged ducts of crawlers of *C. banksiae* reflect better the homology of coccid enlarged ducts with those of eriococcids and pseudococcids than do those of adult female coccids.

If enlarged ducts are plesiomorphic for the three families discussed here, there are major implications for the inclusion of enlarged ducts as a character in systematic studies. The presence or absence of enlarged ducts should not be used as character states in data sets containing representatives with enlarged ducts from only one family since the presence of such ducts may be interpreted as a shared derived character state. A group of plesiomorphic character states may be mistakenly interpreted as shared derived character states if such features are not represented among the outgroups chosen. The result may be an inverted tree topology relative to interpretation as plesiomorphy.

The loss and reduction of features in adult female scale insects is a problem for the phylogenetic study of coccoids. Enlarged ducts may be only one of a number of characters that may be interpreted incorrectly as derived for a particular group, primarily because of loss or non-expression in other taxa or a failure to recognise homology in other groups. Studies of ontogeny, ultrastructure and physiology have the potential to help elucidate the evolution of structures which are commonly described in adult female scale insects and for which homology is otherwise difficult to assess. Thus, a more thorough knowledge of the comparative morphology and function of the cuticular structures of coccoids is essential to the development of a phylogenetically-based classification.

Clearly, the morphology of enlarged ducts is not identical among all taxa discussed since the enlarged ducts of adult females of eriococcids, coccids and pseudococcids are distinguishable. In addition, the setae, ducts and pores surrounding the enlarged duct contribute to the final appearance of the insect's waxy covering and this varies among taxa. Thus, some distinguishing features of the enlarged ducts, such as the shape of the inner end and differences in the sclerotised rims seen in the coccids *C. banksiae* and *P.* sp. near *dodonaeae* may provide informative characters for systematic studies.

Although enlarged ducts may not be useful for distinguishing between *Eriococcus* and *Acanthococcus*, other morphological characters such as the labial features described by Koteja (1974) may prove to be informative at the genus level. This cannot be addressed fully until robust phylogenies, preferably using independent data such as nucleotide sequences, are available to support morphological studies.

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