

THE POSSIBLE EVOLUTION OF THE PLATE-LIKE STRUCTURES ASSOCIATED WITH THE ANAL AREA OF LECANOID COCCOIDEA

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ABSTRACT

Data are presented which strongly support the view of early workers that the anal plates of the Coccidae evolved from anal lobes. In addition, the fate of the anal lobes in other lecanoid families is discussed along with the origin of other plate-like structures associated with the anal area. It is concluded that the anal plates in the family Coccidae and the eriococcid tribe Eriochitonini are an example of convergent evolution and that, with the possible exception of the Aclerdidae, the sclerotised plate-like structures found in other lecanoid families have developed in a different manner.

KEY WORDS: lecanoid Coccoidea, evolution, anal plates, anal lobes.

Some early workers, such as Green (see Steinweden, 1929), postulated that the anal plates typical of the Coccidae evolved from anal lobes which had migrated anteriorly to lie over the anal opening. In addition, there appears to be some doubt as to whether the sclerotised plates found in other lecanoid families (e.g. the Cerococcidae and Lecanodiaspididae) are homologous with the anal plates of the Coccidae. This paper considers the evolution of the anal lobes in a number of lecanoid families and the likely origin of the anal plates in families other than the Coccidae.

The origin of anal plates in the Coccidae and the eriococcid tribe Eriochitonini

Typical first-instar nymphs of many lecanoid Coccoidea have a pronounced anal cleft, bordered by two distinct lobes called anal lobes (Fig. 1). Also typically, each lobe has a single very long apical seta, two short setae on the inner margins and another seta on the outer margin (Fig. 1). This pattern is found in 'typical' Eriococcidae, except that the anal cleft is sometimes rather shallow (see Schmutterer, 1952). However, in several eriococcid genera, the anal lobes tend to become sclerotised in the adult female, a condition well illustrated in several species from Chile by Miller and Gonzales (1975). In a few genera, the anal lobes of first-instar nymphs are also sclerotised (e.g. in *Exallococcus laureliae* Miller and Gonzales) but the distribution of the setae remains similar to the above pattern.

Until recently, the genus *Eriochiton* Maskell was included in the Coccidae on the strength of the presence of a pair of anal plates lying over the anal ring. However, whilst redescribing

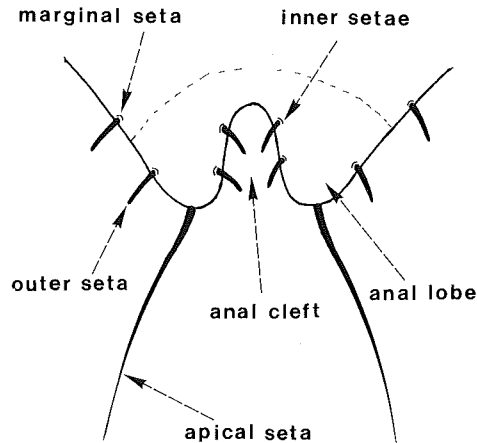


Fig. 1. Typical structure of the posterior end of the abdomen of lecanoid first-instar nymphs with an anal cleft. Note the distribution of the setae.

the adult females of the type species of all genera in the Coccidae, Hodgson (1994a) also studied members of the genus *Eriochiton* and found them to be normal Eriococcidae which had developed anal plates. The genus *Eriochiton* was therefore revised and placed, along with a new genus *Neoerichiton*, in a new tribe, the Eriochitonini (Hodgson, 1994b). The structure of the anal lobes in first-instar nymphs of *Neoerichiton clareae* Hodgson and *Eriochiton hispidus* Maskell is shown in Fig. 2, along with the anal plate areas of second-instar and adult females. It is clear that first-instar nymphs of *N. clareae* have typical anal lobes and that there is no indication of paired anal plates. However, in the second instar, these lobes become more plate-like and, in the adult female, lie over the anal opening in the typical position for coccid anal plates. It is also clear that the number and position of the setae on the anal plates of adult females are similar to those in first-instar nymphs. The situation in *E. hispidus* is slightly different because the anal lobes of first-instar nymphs have already moved a short distance anteriorly and become rather plate-like, although the setae remain the same as in more typical eriococcid first-instar nymphs; in second-instar females, the typical anal plates have moved even further anteriorly, while in the adult female they are still more pronounced, although in both instars the distribution of the setae is as in the first-instar nymph. Thus, it is clear that the anal plates in the Eriochitonini are derived from anal lobes.

In some Coccidae, for example *Bodenheimeria rachelae* (Bodenheimer) (Fig. 3A), the anal lobes of the first-instar nymph are almost identical to those in *N. clareae*, with the same number of rather spinose setae in the same positions. In the second instar, the lobes have moved anteriorly and become more plate-like and one of the spinose setae has moved onto the dorsal surface, while in the adult female the lobes have moved above the anal ring and have a setal distribution similar to that in the second instar. Lambdin and Kosztarab (1973) illustrated the same structures and changes in the closely related *Malloccoccus sinensis* (Maskell). The anal lobes and anal areas of the first and second instars of *Paralecanopsis turcica* Bodenheimer appear to have evolved in a manner similar to that in *Bodenheimeria* and *Malloccoccus*, except that an additional seta appears on each plate in the adult female (Fig. 3B). All three of these genera are here considered to be rather primitive. In the more advanced

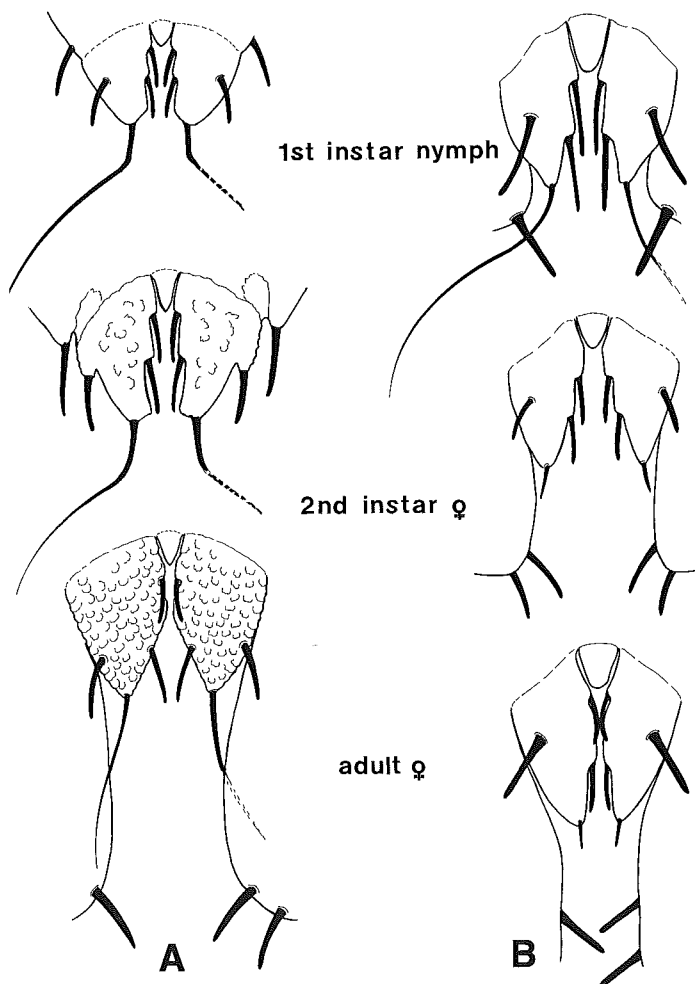


Fig. 2. Anal cleft area of first- and second-instar nymphs and adult female of *Neeriochiton clareae* Hodgson (A) and *Eriochiton hispidus* Maskell (B) (Eriococcidae: Eriochitonini). Note: with increasing maturity (i) the depth of the anal cleft increases, (ii) the anal plates move anteriorly, but (iii) the form and positions of the anal plate setae remain constant.

groups, as in *Protopulvinaria pyriformis* (Cockerell) and *Etiennaea petasus* Hodgson (Fig. 4), the anal plates are well developed even in the first-instar nymph but in all first instars known to the author the distribution of the setae remains constant.

It appears, therefore, that the hypothesis of earlier workers that the anal plates of the Coccidae are derived from the anal lobes is correct. However, it is probably only in the most primitive genera of the Coccidae that the plates have not become differentiated in the first-instar nymph. In addition, it is considered here that genera which have the anterior margin of the anal plates only poorly demarkated from the dorsum (as in *Bodenheimeria*) and/or have spinose setae on the anal plates similar to marginal setae are probably primitive.

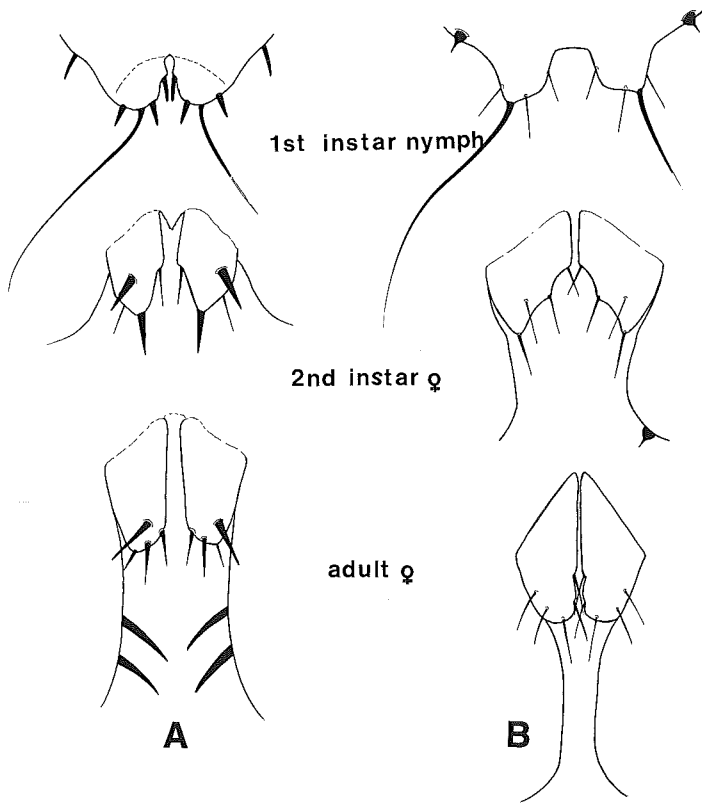


Fig. 3. Anal cleft area of first- and second-instar nymphs and adult female of *Bodenheimera rachelae* (Bodenheimer) (A) and *Paralecanopsis turcica* Bodenheimer (B) (Coccidae). Note that the changes during ontogeny are similar to those in Fig. 2.

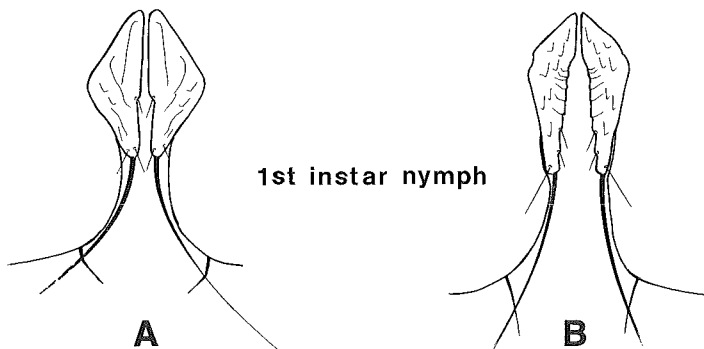


Fig. 4. Anal cleft area of first-instar nymphs of *Protospulvinaria pyriformis* (Cockerell) (A) and *Etiennaea petasus* Hodgson (B). Note: (i) how the anal plates are already well developed in the first instar, but (ii) the position of the setae remains the same as in Fig. 1.

The origin of anal plate-like structures in other lecanoid Coccoidea

Two types of sclerotised plates are found in the other lecanoid Coccoidea: (i) a single plate lying dorsally over the anterior end of the anal cleft, as in the families Acleridae, Cerococcidae, Lecanodiaspididae and some Eriococcidae, and (ii) paired plates or areas of sclerotisation which lie along the inner margins of the anal lobes and which may be joined ventrally beneath the anal ring, as in the family Lecanodiaspididae and in a few Acleridae.

(i) *The single dorsal plate.* Typical first-instar nymphs of the Acleridae have the usual long seta apically and 2–3 (often rather thickened) setae present on the dorsal surface near the base of the anal cleft (Fig. 5) (McConnell, 1953; Howell, 1973). However, in *Aclerda pasquieri* Balachowsky, the anal lobes of the first-instar nymph are clearly separated from the preceding segment by a deep indentation and are fused together over the anal opening (Fig. 5B) (McConnell, 1953); in addition, the nymphs have three pairs of setae dorsally as well as the long apical seta. Later instars have only been described for one species (*A. tillandsiae* Howell), but in this species the apical seta seems to disappear and the two pairs of thickened setae in the first- and second-instar nymphs are joined by two pairs of short setose setae in the third instar, becoming four pairs of long setose setae in the adult female (Howell, 1973) (Fig. 5A). Similar arrangements are illustrated for other *Aclerda* species (McConnell, 1953), although the number of long setae may vary and the dorsal plates may be deeply cleft. It looks, therefore, as though part or all of the anal lobes move forward over the anal ring and fuse to form a single central plate during the ontogeny of the Acleridae. In addition, this central plate is often cleft at the posterior end, also suggesting its double origin. The Acleridae are often

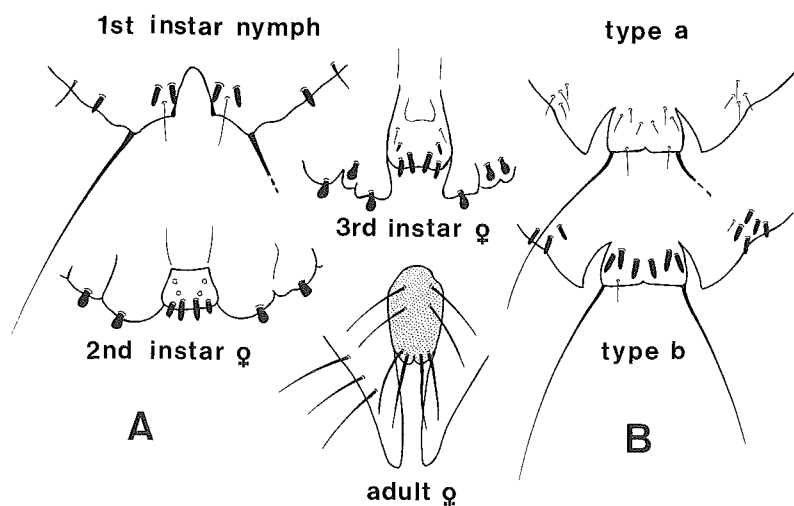


Fig. 5. A. Anal cleft area of the first-, second- and third-instar nymphs and adult female of *Aclerda tillandsiae* Howell (after Howell, 1973). Note how, with increasing maturity, (i) the 2 pairs of fleshy setae move onto a central plate-like structure and (ii) that this appears to become the dorsal plate in the adult female. B. Anal cleft area of the first-instar nymphs of the two forms of *Aclerda pasquieri* Balachowsky (after McConnell, 1953). Note how in both forms: (i) the anal lobes appear to have become fused medially, (ii) they are clearly separated from the rest of the abdomen by a deep groove, and that (iii) the anal plate setae are all present on the dorsal surface.

considered to be the lecanoid family most closely related to the Coccidae (Borchsenius, 1958; Boratyski and Davies, 1971; Koteja, 1974; Miller and Kosztarab, 1979; Danzig, 1980; Miller, 1984 and Koteja (in Kosztarab and Kozár, 1988)). The development of the dorsal anal plate in the Acleridae appears, therefore, to have some parallels with the development of the anal plates in the Coccidae but it is here considered that, whilst these two families may be more closely related to each other than to other lecanoid families, this relationship is still rather distant.

In the other families with a central dorsal plate, the plate appears to have no association with the anal lobes but to be formed from a posterior extension of the dorsum. For instance, members of the Eriochitonini already have a small central plate present in first-instar nymphs, which persists throughout development into the adult female (Fig. 2). This plate may even be present in many Coccidae as a small sclerotised ridge lying at the anterior end of the anal clefts between the two lateral anal plates, e.g. in second-instar females of *B. rachelae* (Fig. 3).

In the Cerococcidae (Hamon and Kosztarab, 1979) and Lecanodiaspididae (Williams and Kosztarab, 1970), a sclerotised plate is already present above the anal ring in first-instar nymphs (Fig. 6A and 6B, respectively). However, the anal lobes are also present and complete, with more or less the typical number of setae in the usual positions. It is therefore considered here that the dorsal plate is not derived from the anal lobes but has developed from a posterior extension of the dorsum, as in the Eriochitonini.

(ii) *The lateral plates.* Lateral anal plates are present in the Lecanodiaspididae (Fig. 6B) (Williams and Kosztarab, 1970). The first-instar nymphs of this family have quite pronounced anal lobes, each lobe with a distinct triangular area of sclerotisation at the anterior end of the anal cleft near its inner margin. It is considered here that these plates are not homologous to the anal plates of the Coccidae because (i) the long apical seta and at least two of the shorter setae are quite separate from the plates, (ii) the inner margin of each plate lies below the anal ring, where (iii) they become fused to form a sclerotised 'bow-tie' shaped bar in the adult female.

The inner margins of the anal cleft of the Acleridae are also slightly sclerotised (McConnell, 1953; Howell, 1973) (Fig. 5). The fate of this sclerotisation in later instars is still unclear, although Howell (1973) illustrates some sclerotisation of the inner margins in the later instars.

The evolution of anal plates in the other lecanoid Coccoidea

As lecanoid Coccoidea are thought to have evolved from the Archeococcoidea which lack an anal cleft, it is likely that the more primitive lecanoid families will also lack an anal cleft. The Pseudococcidae are generally considered to be primitive lecanoid coccids and they lack an anal cleft, although the anal lobes are clearly indicated in first-instar nymphs by the presence of a long apical seta (Fig. 6G). In addition, there are two spinose setae on this lobe that could represent the two setae on the inner margin of the anal cleft (Fig. 1).

The Cryptococcidae and Kermesidae are also generally considered to be more or less primitive. In the first-instar nymphs of the Cryptococcidae, there is no anal cleft and the anal lobes are very small or absent, although there is a long apical seta and 2–3 rather spinose setae associated with it (Kosztarab and Hale, 1968; Williams, 1985) (Fig. 6E). It is unclear what becomes of these setae in later instars. In the Kermesidae, the structure of the anal area of first-instar nymphs is similar to that of the typical crawler and is frequently sclerotised as in

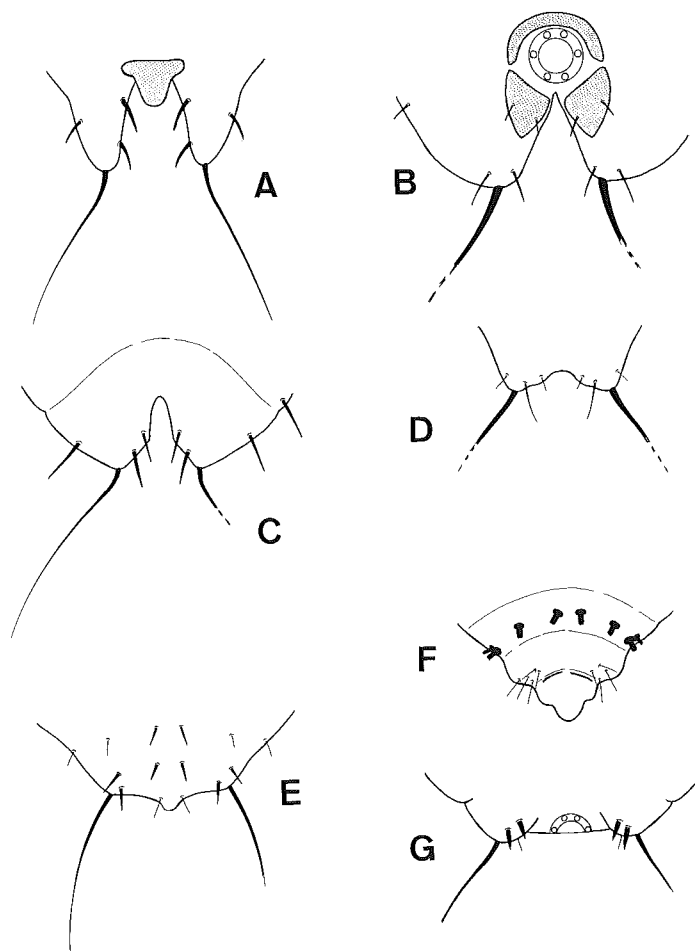


Fig. 6. Posterior ends of the abdomen of first-instar nymphs of: the Cerococcidae (A) (after Hamon and Kosztarab, 1979); the Lecanodiaspididae (B) (after Williams and Kosztarab, 1970); the Kermesidae (C) (after Baer and Kosztarab, 1985); the Asterolecaniidae (D) (after Russell, 1941); *Cryptococcus williamsi* Kosztarab and Hale (E) (after Kosztarab and Hale, 1968); *Dactylopius coccus* Costa (F) (after Guerra and Kosztarab, 1992), and the Pseudococcidae (G) (after Miller, 1974, 1975, 1983).

some Eriococcidae (Baer and Kosztarab, 1985) (Fig. 6C). In the adult female, the lobes come to lie in a variety of positions: they "...may surround the anal ring, be located ventral to it or be located dorsal to it. If situated either around or ventral to the anal ring, they are usually membranous. If located dorsal to the anal ring, they are triangular, plate-like and sclerotised" (Bullington and Kosztarab, 1985, p. 24). The Kermesidae are thus rather diverse and more intermediate instars need to be studied for a better understanding of this family.

The anal lobes of first-instar Asterolecaniidae (Russell, 1941) are very small or even absent in some genera (e.g. *Grammococcus* Miller and Lambdin). The number of setae and their

position vary between species, although apparently there is always a long apical seta, and this and the other setae appear to remain through to the adult stage (Fig. 6D).

Anal lobes appear to be entirely absent in the first-instars of the Dactylopiidae but may be represented by lateral lobes rather like cerarii, reminiscent of the Pseudococcidae (Guerra and Kosztarab, 1992) (Fig. 6F).

In the first-instar nymphs of the diaspid families, the anal area has been modified into a pygidium. This is also true of the Conchaspidae, where the posterior end of the abdomen in the first instar is pygidial-like and strongly reminiscent of the Diaspididae (D'Ascoli and Kosztarab, 1969).

As I have been unable to locate descriptions of first instars of the remaining lecanoid families Kerriidae, Stictococcidae and Beesoniidae, the ontogeny of their anal lobes cannot be discussed here.

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