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Preliminary phylogeny of some non-margarodid Coccoidea (Hemiptera) based on adult male characters

Abstract - A series of phylogenetic analyses was undertaken using 144 characters from macropterous males of 94 taxa in 16 families of non-margarodid Coccoidea, with Ortheziidae as outgroup. The results are presented and discussed. Although there is good bootstrap support for most of the traditional family groupings, support for inter-family relationships is poor or absent. However, in almost all trees, the Stictococcidae were sister to the Beesoniidae, the Conchaspidae were sister to the Diaspididae and the Aclerdidae were sister to the Coccidae, although there is no bootstrap support for this last grouping. The Pseudococcidae and Eriococcidae were never monophyletic. The analyses also suggested that *Puto* and *Phenacoleachia* might be closely related.

Key words: *Inglesia patella*, Dactylopiidae, Kermesidae, Lecanodiaspididae, Asterolecaniidae, Cerococcidae, Kerriidae.

INTRODUCTION:

The use of cladistic analyses to determine possible relationships within the Coccoidea have been few (Miller, 1984 (major portions of the Coccoidea); Miller & Miller, 1993a, 1993b (*Eriokermes* and *Puto*); Foldi, 1995 (*Limacoccus*); Miller, D.R. & Williams, 1995 (Micrococcidae); Miller, G.L. & Williams, 1995 (adult males of the *Toumeyella* group); Qin & Gullan, 1995 (Ceroplastinae); Hodgson & Henderson, 1996 (*Eriochiton*); Foldi, 1997 (many families); Miller & Hodgson, 1997 (lecanoid families, particularly Coccidae); Gullan & Cook, 2001 (*Dactylopius*), and Gullan & Sjaarda, 2001 (margarodids)). Most of these analyses were based on characters taken from a range of life stages, generally including a few male characters. However, stages such as the adult female are so different in each family that the homologies of the structures can, at best, be uncertain, whilst many characters of some significance in one family are absent in another. Such problems are much reduced in the macropterous males, which have undergone much less evolutionary change and on which the homologies of the various structures are more certain. Indeed, in a recent paper (Hodgson & Millar, in press), the authors found that the only way they could approach the phylogenetic

relationships of an unusual female aceridid which had fully-developed legs (apart from using molecular techniques) was by studying the adult males.

The present study is a first attempt to look at the possible phylogeny of a large group of the non-margarodid Coccoidea using only male characters. Most previous phylogenetic analyses have used just one species for each taxon. As our current knowledge of males is still relatively poor, it is not possible to be certain which characters might be purely species characters and which might actually diagnose higher taxa. To overcome this, in almost all instances, a minimum of 2 species per higher taxon was used in this study, while most had between 3 and 5 species and the largest families up to eleven.

MATERIALS AND METHODS

Four species of Ortheziidae were used as the outgroup. The ingroup included a further 90 taxa belonging to 16 families and these are listed in Appendix A, along with the sources of the data. The initial analyses used 144 characters. There is no room to include a list of characters and character-states but the author will willingly provide these (plus the character matrix) to anyone interested. The analyses were run using PAUP*4.0b7 (Swofford, 2001) and Hennig86 (Farris, 1988). All characters were equally weighted and unordered. For the PAUP* analyses, 1000 random edition sequence replicates were run using stepwise addition and TBR, with the MultiTrees option in effect. For the Hennig86 analyses, the "mhennig" option was used (constructs several trees, each by a single pass, adding the terminals in several different sequences; the shortest trees are retained), followed by the "bb" option (applies extended branch-swapping to the trees in the current tree file, retaining only the shortest trees). Where necessary, strict consensus trees were generated using "nelson". Some Hennig86 analyses used *a posteriori* successive weighting (this weights characters according to the *ci* from the previous analysis).

The Hennig 86 analyses were run using various combinations of taxa and characters; where these produced significant changes to the preferred structure (Fig. 1), these are mentioned in the text. Whilst some analyses used all 144 characters, other analyses used fewer characters, the characters with the greatest number of steps and/or the lowest consistency index (*ci*) having been removed.

RESULTS AND DISCUSSION

It needs to be stressed that these analyses are preliminary; whilst there was good bootstrap support for most families, the support for the relationships between families was generally poor. Nonetheless, some interesting relationships emerged from this study.

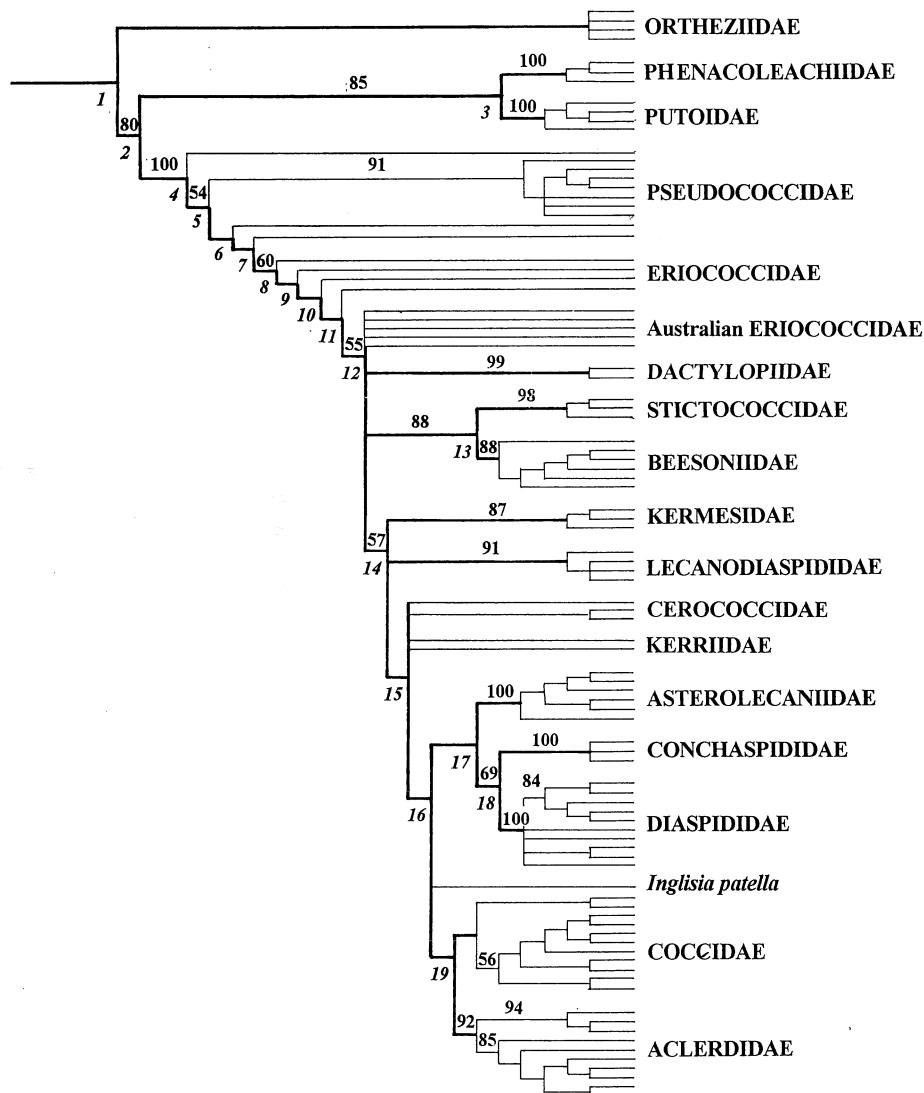


Fig. 1 - A strict consensus cladogram from approximately 500 equally parsimonious trees using PAUP*, with 1000 random addition sequence replications, 94 taxa and 144 characters; character-states unordered; Length 1508, CI 19; RI 71. Fifty-percent bootstrap values above the line; node numbers in italics below line on left of each node. Note that the following sister groups appeared in this and almost all other cladograms: (i) Coccidae + Aclerdidae (Aclerdinae + Rhodesaclerdinae (Hodgson & Miller, in press)); (ii) Diaspididae + Conchaspidae, and (iii) Beesoniidae + Stictococcidae. In no analysis was the Pseudococcidae and Eriococcidae monophyletic.

The PAUP* analysis, based on 1000 random sequence replications, produced over 500 minimum-length trees (*CI*: 0.185, *RI*: 0.712, Length 1508) and the strict consensus tree is presented in Fig 1. In this and most other analyses done for this study, most families were monophyletic, the exceptions being (a) the Pseudococcidae, where *Paracoccus*, *Ceroputo* and *Nairobi* usually fell outside the main pseudococcid clade; (b) the Eriococcidae, which never formed a clade, and (c) the Coccidae, where *Inglisia patella* Maskell usually fell outside the clade containing the Aclerdidae and Coccidae (as in Fig. 1). *I. patella* is a very unusual coccid (based on both adult female as well as adult male characters) and perhaps should not be included in the Coccidae. In addition, a small clade of four coccid species sometimes became detached from the main Coccidae clade (see under node 19 below).

The relationships of the various taxa will be discussed by reference to the node numbers in Fig. 1.

Node 3. This analysis suggests that the Putoidae and Phenacoleachiidae might be closely related. In all analyses, these were sister taxa and often formed a clade, as in Fig. 1. The males of *Phenacoleachia* have abdominal spiracles (although they are very small and extremely difficult to see), which might place them in the archaeococcoids but male *Puto* lack abdominal spiracles; the absence of compound eyes also suggests that their placement with the archaeococcoids is questionable.

Nodes 4-7. As indicated above, the Pseudococcidae were never monophyletic. *Paracoccus* was usually sister to all other ingroup taxa included here except *Puto* and *Phenacoleachia* (node 4 in Fig. 1) while *Ceroputo* and *Nairobi* frequently arose from the 2 nodes immediately above the rest of the pseudococcids (nodes 6 & 7 in Fig. 1).

Nodes 8-11. Only four species of “typical” eriococcids were included in this study (*Eriococcus buxi* (Fonscolombe), *E. orariensis* Hoy, *Eriochiton armatus* Brittin and *Gossyparia spuria* (Mod.)), but these almost never formed a clade but arose separately, as in Fig. 1. In a later study, a further five species of eriococcids were added but none formed a clade. These relationships will require further study. This group of taxa were sister to all other taxa included in this study, bar the pseudococcids, putoids and *Phenacoleachia*. The “odd” Australian eriococcids (*Apiomorpha*, *Cystococcus*, *Lachnodius* and *Opisthoscelis*) rarely formed a clade but were variously associated with the Dactylopiidae and the stictococcid/beesoniid clade and node 14, as at node 12 in Fig. 1. The “typical” eriococcids did not appear to be closely related to the “odd” Australian taxa.

Node 12. From this node arises the unusual Australian genera *Apiomorpha*, *Cystococcus*, *Lachnodius* and *Opisthoscelis* (generally classified as Eriococcidae), the Dactylopiidae, a clade which has the Beesoniidae and Stictococcidae as sister groups (node 13) and all taxa included in node 14. Although the close relationship between the Beesoniidae and Stictococcidae would appear to be unlikely based on their biology and other life stages, it was constant throughout the current series of analyses and had a bootstrap value of 88. The only previous study which included both the Beesoniidae and Stictococcidae (Foldi, 1997 - using a wide range of characters from all stages) placed these taxa apart but arising from nodes near the apex of the tree, whilst in this

study, they usually arose from a much more basal node. Miller & Hodgson (1997), using many characters from the 1st-instar nymph and adult female but also a few from the adult male, also considered that the Stictococcidae might have arisen from a more basal node, close to the Kermesidae and Eriococcidae. Interestingly, an analysis of nucleotide sequences (from the nuclear small-unit ribosomal RNA gene (SSU rRNA) derived from 39 species belonging to 14 putative families of scale insects, using aphids as outgroups) (Cook *et al.*, submitted) also found the Beesoniidae and Stictococcidae to be sister-groups but arising from the apical node and, indeed, in the present Hennig86 analyses, this clade also occasionally arose from the apical node when few characters were included in the analysis or when the characters were weighted.

The unusual Australian eriococcid genera (*Apiomorpha*, *Cystococcus*, *Lachnodius* and *Opisthoscelis*) plus the Dactylopiidae were also frequently associated in the other analyses in this study. While the dactylopiids were not always linked to the Australian eriococcids, they were never in a clade with the Eriococcidae *sensu stricto*, to which they have sometimes been linked (Gullan & Cook, 2001).

Node 14. Three clades arose from this node, namely the Kermesidae and Lecanodiaspididae and the taxa on node 15. Whilst this arrangement was frequent in other analyses made in this study, the exact arrangement of the Kermesidae, Lecanodiaspididae, Cerococcidae and Kerriidae (plus the Asterolecaniidae) tended to vary and the bootstrap values supporting any particular arrangement were poor. However, these five families usually arose close to one another within the main body of the tree.

Node 15. This includes the Cerococcidae, Kerriidae and the taxa on node 16. As noted for node 14, the exact relationships of the Kermesidae, Lecanodiaspididae, Cerococcidae and Kerriidae did vary considerably between analyses. However, in Fig. 1, neither the Cerococcidae nor the Kerriidae form a single clade.

Node 16. This clade consisted of two other major clades (nodes 17 and 19) plus *Inglesia patella*.

Node 17 has the Asterolecaniidae as a sister group to node 18, the conchaspidid/diaspidid clade. In many of the other analyses done in this study, the asterolecaniids are more closely related to the Cerococcidae, Lecanodiaspididae and Kerriidae and, indeed, there is no bootstrap support for its sister relationship with the conchaspidid/diaspidid clade. Nonetheless, if this relationship was found to be supported by other data, it would be very interesting as these three families (the Asterolecaniidae, Conchaspidae and Diaspididae) do not produce honeydew and are therefore probably all non-phloem feeders, unlike most of the other families included here.

Node 18 has the Conchaspidae and Diaspididae as sister groups. This clade occurred in almost all analyses done for this study. In the only previous phylogenetic analysis in which the Conchaspidae were included (Foldi, 1997), the family arose from a more basal position even than the Pseudococcidae. Koteja (1974), in his studies on the structure of the labium of the Coccoidea, also considered that the Conchaspidae arose from a basal node within the non-margarodid coccoids, although

this was not based on a cladistic analysis. Previous studies, based mainly on adult female and nymphal characters, have the diaspidids arising from an apical node but, in many analyses done for the present paper, this clade arose from a more basal node, even close to the stictococcid/beesoniid clade. In another cladistic analysis, using only male characters (Gullan & Cook, 2001), it was also found that the Diaspididae arose close to the eriococcid node; and, in the analysis of nucleotide sequences mentioned above (Cook *et al.*, submitted), the diaspidids were in a clade with the dactylopiids and eriococcids, although the relationship was poorly supported. Unfortunately, the latter study did not include the Conchaspidae. Whilst the conchaspidid/diaspidid clade was reasonably well supported in Fig. 1, with a bootstrap value of 69, this relationship is somewhat surprising.

Node 19. In all cladograms in this study, the coccids and the aclerdids formed a single, usually apical clade although there is no bootstrap support for this relationship. However, previous analyses, using other growth stages, have also frequently suggested this relationship. In the present study, *Inglisia patella* rarely fell within the Coccidae clade and was often placed even outside the aclerdid/coccid clade, as in Fig. 1. In the Hennig86 analyses, when fewer characters were used or the data was weighted, the Coccidae often became polyphyletic, with the clade formed from *Eulecanium tiliae* (Linnaeus) + *Alecanochiton* sp. + 2 *Pounamococcus* species arising from a much more basal node, close to the Lecanodiastidae. These purported relationships need to be further studied but the males of these four species have hamulohalteres which are absent from the other soft scales included in this study. Whilst the genera with hamulohalteres may well be more primitive than the other soft scales included here, there is no reason (based on studies using other life stages) to believe that they belong to different families. Thus, the preferred trees were those in which most families (but particularly the Coccidae) were monophyletic. With regard to the Aclerdidae, a recent study (Hodgson & Millar, in press) considered the relationships within the Aclerdidae and concluded that *Rhodesaclerda* McConnell did belong in this family and this was confirmed in the present study, where the bootstrap support for the Aclerdidae was 100.

It is clear that these analyses have not provided a single most-likely phylogeny, although the approximate relationships of most families appeared to be reasonably fixed. The preferred trees were not dissimilar to many that had been produced using other life stages, except that the Diaspididae appeared to be linked with the Conchaspidae and that these sister taxa were not always at the apex of the tree but arose much closer to the eriococcids, usually as a separate dichotomous branch. This finding is somewhat surprising and it will be interesting to see what relationships molecular studies suggest in the future. Only in the unpublished paper of Cook *et al.* (submitted) has the Beesoniidae and Stictococcidae been considered as possible sister groups; on the basis of that paper and this study, they appear to be most closely related to the Australian eriococcids. The finding that the Aclerdidae and Coccidae are sister groups is not new and has been suggested by most previous phylogenies.

Appendix A: species used and sources of data for phylogenetic analyses

The data taken from species marked with an asterisk (*) are new and taken from slides. Data for the species without an asterisk were taken from the publications indicated:

Aclerdidae: Aclerdinae: (7): *Aclerda arundinariae* McConnell*, *A. distorta* Green*, *A. tillandsiae* Howell*, *A. tokionis* (Cockerell)*, plus 2 unidentified *Aclerda* sp.* and a new species from South Africa*; Rhodesaclerdinae: (3): *Rhodesaclerda combreticola* McConnell* plus 2 new species from southern Africa*.

Asterolecaniidae (6): *Asterolecanium delicatum* (Green)*, *A. penicillatum* Russell*, *A. ungulatum* Russell*, *A. vulgaris* Russell*, *Asterodiaspis album* (Takahashi)*, *Hsuia cheni* Borchsenius*.

Beesoniidae: (6): *Beesonia dipterocarpi* Green*, *Gallococcus secundus* Beardsley, *Mangalorea hopeae* Takagi* plus unpublished figures of 3 new species (Takagi, 1992).

Cerococcidae (3): *Cerococcus artemesiae* Cockerell*, *C. indicus* (Maskell)*, *C. ornatus* Green*.

Coccidae (12): *Alecanochiton* sp., *Ceroplastes beroliniae* (Hall), *Coccus hesperidum* L., *Eriopeltis* sp., *Eulecanium tiliiae* (L.), *Inglisia patella* Maskell*, *Inglisia theobromae* (Newstead), *Luzulaspis luzulae* (Dufour), *Plumochiton pollicinus* Hodgson & Henderson*, *Poropeza dacydii* (Maskell)*, *Pounamococcus cuneatus* Henderson & Hodgson*, *P. tubulus* Henderson & Hodgson* (Giliomee, 1967).

Conchaspidae (3): *Conchaspis angraeci* Cockerell*, *C. socialis* Green*, *C. vayssierei* Mamet*.

Dactylopiidae: (2): *Dactylopius* sp., *Dactylopius confusus* (Cockerell) (Loubser, 1966).

Diaspididae: Parlatorini: (2): *Parlatoria oleae* (Colvée), *P. blanchardii* (Targioni-Tozzetti); Aspidiotti: (3) *Abgrallaspis cyanophyllii* (Signoret); *Aspidiottus hederae* (Vallot), *A. destructor* Signoret; Diaspidini (4): *Chionaspis salicis* (L.), *Diaspis boisduvalii* Signoret, *Lepidosaphes ulmi* (L.), *Pseudaulacaspis pentagona* (Targioni-Tozzetti); Odonaspидini (1): *Rugaspidiotus tamaricicola* (Malenotti) (Ghauri, 1962).

Eriococcidae: (9) *Eriochiton armatus* Brittin*, *Eriococcus buxi* (Fonscolombe), *E. orariensis* Hoy, *Gossyparia spuria* (Mod.) (Afifi, 1968); plus five atypical Australian "eriococcids": *Apiomorpha spinifer* Froggatt*, *Cystococcus echiniformis* Fuller*, *Lachnodius eucalypti* (Maskell)*, *Opisthoscelis verrucula* Froggatt*, *O. subrotunda* Schrader*.

Kerriidae (2): *Tachardiella* sp.*, *Tachardiella aurantiaca* (Cockerell)*.

Kermesidae: (3): *Kermes quercus* (L.) (Koteja & Zak-Ogaza, 1972); *K. bytinskii* Sternlicht (Sternlicht, 1969); *Eriokermes gillettei* (Tinsley) (Miller & Miller, 1993a).

Lecanodiaspididae (4): *Lecanodiaspis acaciae* (Maskell), *L. africana* Newstead, *L. anomola* Green (Afifi & Kosztarab, 1969); *L. elytropappi* (Munting & Giliomee) (Munting & Giliomee, 1967).

Ortheziidae: (4): *Orthezia* sp.*, *Orthezia urticae* (L.), *Orthezia* sp., *Newsteadia floccosa* de Geer (Koteja, 1986).

Phenacoleachia (3): unidentified *Phenacoleachia* sp. (probably *zealandica* Maskell) plus two possibly new species*.

Pseudococcidae (10): *Ceroputo pilosellae* _ulc, *Dysmicoccus alazon* Williams, *Ferrisia virgata* (Cockerell), *Nairobi bifrons* De Lotto, *Nipaecoccus nipae* (Maskell), *Octococcus africanus* (Brain), *Paracoccus glaucus* (Maskell)*, *Planococcus citri* (Risso), *Pseudococcus viburni* (Signoret), *Saccharicoccus sacchari* (Cockerell) (Afifi, 1968).

Puto (4): *Puto arctostaphyli* Ferris*, *P. kosztarabi* Miller & Miller*, *Puto yuccae* (Coquillett)*, *Puto* sp*.

Stictococcidae (3): *Parastictococcus brachystegiae* Hall*, *P. gowdeyi* Newstead*, *P. multispinosus* (Newstead)*.

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