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Phylogeny and classification of the Margarodidae and related groups (Homoptera: Coccoidea)

The classification of the group usually categorized as the family Margarodidae has been of interest for many years. MORRISON (1928) considered the family to consist of five subfamilies. Others have divided the group in various ways including seven subfamilies (OBENBERGER 1957), two families (FERRIS 1957), and six families (KOTEJA 1974).

Margarodids originally were characterized by MORRISON (1927) as consisting of taxa that have abdominal spiracles in all or most stages and have compound eyes as adult males. Based on the methods of HENNIG (1966), it is clear that these character states cannot be used to diagnose the family. They occur in all major groups of the Sternorrhyncha outside of the Coccoidea and therefore most likely are primitive. Without further justification of the group, the family Margarodidae would have to be abandoned as paraphyletic or polyphyletic.

In recent years characteristics of the anal region and to some extent the mouthparts have been used to distinguish the margarodids from other scale insect families. Considering that these characters show as much or more diversity of structure within the Margarodidae as they show within all of the rest of the Coccoidea and in light of the questionable diagnostic features of the family, I decided to investigate the relationships of specified margarodid subunits by comparing them with other scale-insect groups.

Methods. A phylogenetic analysis was undertaken using the WAGNER algorithm (FARRIS 1970, FARRIS et al. 1970) component (WAGTREE) of the PHYSYS program developed by FARRIS and MICKEVICH. I am very grateful to Steve FARRIS and Mary MICKEVICH for their generous assistance in running my data on PHYSYS.

The character matrix includes data from first instars, adult males, adult females, sperm, symbionts, sex-determining mechanisms, and life-history information. The matrix consists of 103 characters and 39 taxa. Choice of the rank of the taxonomic units to be studied was dependent upon the likelihood of group monophyly. For example, there appeared to be several distinct units within the Margarodidae suggesting the possibility that it is polyphyletic. To overcome this problem, subordinate units were selected that reasonably could be considered to be monophyletic. In the case of the Acleridae, there is strong evidence that the family is monophyletic, and it therefore was used as the analysis unit.

In forming character-transition series, objectivity was a primary goal. Determination of the primitive state was achieved by outgroup comparison with the Aphididae. Transition series initially were evaluated in as logical a manner as possible (e.g., 1 seta to 2 setae to 3 setae; not 1 seta to 3 setae to 2 setae). Similarly appearing character states were scored the same regardless of any preconceived ideas (e.g., anal lobes absent in margarodids and diaspidids would be given the same designation; they would not be considered to be secondarily lost in the Diaspididae).

Only a single analysis of the data has been run. It is critical that the character transformations be reevaluated in light of the structure of the tree; this process undoubtedly will increase the fitness of the data to the tree and likely will cause some minor structural changes.

Because of space constraints it has not been possible to present character data. I will be happy to provide this information on request.

Results. It is important to remember that these results are preliminary. The step in which

the characters are reevaluated has not been completed and is important in finalizing the analysis. The PHYSYS program produced eight equally parsimonious trees. Differences in the trees were relatively minor and primarily involved interchange of subunits of the Margarodinae. The tree presented in Figure 1 is an Adams consensus tree (ADAMS 1972) of the eight equally parsimonious trees. The Consistency Index for each of the eight trees is .33, but this likely will be increased through character reevaluation.

The structure of the tree in Figure 1 generally is compatible with the classification accepted by most current coccidologists. As suggested by previous workers the scale insects have two primary divisions each of which has become independently quite specialized at its terminus. In the past, these groups have been called the Archeococcoidea or Orthezioidae and the Neococcoidea or Coccoidea and were characterized by the presence or absence of abdominal spiracles. As might be anticipated, the characterization of the Archeococcoidea with a primitive character state has caused problems. In the tree given by BORATYNSKI and DAVIES (1971) the Archeococcoidea are paraphyletic and the Neococcoidea are polyphyletic. The tree in Figure 1 divides the scale insects into two primary groups: A lineage that includes the Margarodidae only and a lineage that encompasses all other scale insects including the Ortheziidae, Phenacoleachidae, Putoidae, Pityococcus-McKenzie, the lecanoids, and the diaspidoids. The advanced condition "lack of abdominal spiracles" is a useful character state, but it does not diagnose a currently accepted major scale taxon.

The Margarodidae, with the exception of Pityococcus, are a monophyletic group. Three of the subfamilies proposed by MORRISON (1927) are natural subunits and could be given the same designations as before (i.e., Margarodinae, Monophlebinae, and Steingelinae).

The Xyloccocinae as understood by MORRISON (1928) are very different from the groupings that can be derived from the tree in Figure 1. Matsucoccus Cockerell is not associated with Xyloccoccus Low but instead is closely related to the Steingelinae and, in fact, reasonably could be placed in that subfamily. BEARDSLEY's (1968) suggestion that Matsucoccus be treated as a separate subfamily also is consistent with the tree structure. Kuwanla Cockerell and Neosteingelia Morrison form a group separate from the Xyloccocini and cannot be considered as part of the Margarodinae (as suggested by MORRISON 1928) without also including the Steingelinae and Matsucoccus.

Eight genera of the Margarodinae were analyzed as a test of JAKUBSKI's (1965) hypothesis that the subfamily contains a separate, convergent family (i.e., the Termitococcidae). Unfortunately, specimens of Termitococcus Silvestri were not available, but adults and first instars of Eurhizococcus Silvestri, the other genus in the Termitococcidae, were studied. It is evident from the analysis that Eurhizococcus is an unusual but well integrated part of the Margarodinae. The fossorial margarodids, though quite divergent in some features, form a well-defined, natural group.

It is interesting that Steingelia, which has been suggested to be a relative of the Coccidae (GLIOME 1967), and Matsucoccus, which has been hypothesized as closely related to the Ortheziidae (BEARDSLEY 1968), are closely related to one another and are integral part of the margarodid lineage.

The Coelostomidinae are not a monophyletic unit. The genera Coelostomidia Cockerell and Ultracoelostoma Cockerell are closely related to the Monophlebinae and could be included in that subfamily. The genera Mimosicerya Cockerell and Paracoelostoma Morrison as a "unit" are paraphyletic. Based on this analysis they must be treated as separate groups. Callipappus Guerin-Meneville, which is treated by MORRISON (1928) as a tribe of the Margarodinae, clearly is not part of that subfamily. Its placement, like parts of the Coelostomidinae, is unclear. It is considered to be a distinct unit in this analysis. A separate Callipappinae has been recognized elsewhere (OBENBERGER 1957).

Examination of the other main lineage (the Neococcoidea lineage) demonstrates several interesting relationships. Four groups of soft scales were studied (i.e., the Eulecanium group, Inglisia group, Coccus group, and Eriopeltis group). As anticipated they form a natural unit and are closely related to the Acleridae.

Even though first instars of eriococcids and kermesids are remarkably similar, these similarities are primitive character states and do not define a group; based on other characters the Eriococcidae and Kermesidae must be considered to be separate families. The alternative would be for them to be part of a group consisting of the aclerids, coccids, eriococcids, and kermesids. For this analysis "Eriococcus" gillettei Tinsley was treated as a separate analysis unit since the adult males share derived character states with kermesids and because adult females have discoidal pores and 9- or 10-ocular pores-features of kermesids not eriococcids. As suspected, this

species and very likely "E. juniperi Goux and "E. juniperinus De Lotto are kermesids.

The Putoidae are a well-defined group and should be treated as a monophyletic unit separate from the Pseudococcidae. Phenacoleachiidae also are a separate group.

The genus Pityococcus, which has been considered to be a margarodid, was treated as a separate analysis unit because the adult male has ostioles, a derived character state typical of pseudococoids, putoids, and phenacoleachids. This character in addition to the occurrence of pseudococcid-type circuli and tubular ducts causes there to be no surprise that the analysis placed Pityococcus separately from the Margarodidae. This unusual genus, and probably Electrococcus Beardsley and Desmococcus McKenzie, are a group comparable in rank to the putoids and phenacoleachids.

The Ortheziidae are the most primitive group on the Neococcoidea lineage. Although this family has been associated with the Margarodidae based on shared primitive characters, the presence of the derived state of a well-developed, setaceous, and poriferous anal ring lends credence to its association with the Neococcoidea.

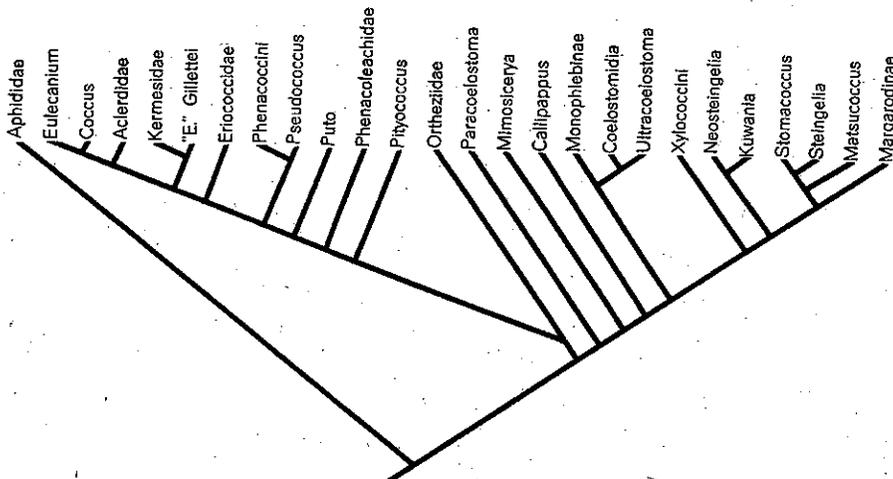


Fig. 1. Lower groups of the Coccoidea

Because it has not been possible to give details of the character data, it seems of value to discuss the distribution of one or two features as examples of the data set. Life-history data similar to that presented by DANZIG (1980) fit the tree remarkably well. The primitive condition of four female instars and five male instars, including a single pupal stage, occurs in the non-cyst forming margarodid groups, the ortheziids, and Pityococcus. The highly specialized, cyst-forming groups form a distinct, well-defined unit within the Margarodidae including the Margarodinae, Steingelinae, Xylococcus, Matsucoccus, Neosteingelia, and Kuwania. The only apparent discrepancy is Pityococcus which should not form a cyst or should do so in a slightly different way than the rest of the cyst formers. Taxa on the lower portion of the Neococcoidea lineage possess the primitive state; a second pupal stage appears near the Puto node, and the loss of a female instar occurs in the Ericoccidae. Character transitions of sex-determining mechanisms also fit the tree. The XX-XO system is the primitive state and occurs in the margarodid lineage, the Ortheziidae, and Puto. The lecanoid system first appears in the ancestor of the pseudococoids and begins a transition to the comstockiella system in the Ericoccidae. In contrast to earlier statements (MILLER and KOSZTARAB 1979) the lecanoid system did not develop independently on two unrelated lineages. NUR (1980) has been a strong proponent of the monophyletic origin of the lecanoid system. The structure of the anal tube and anal opening is useful. It is a complex, multistate character that is diagnostic of the Margarodidae and other smaller units.

Some characters do not fit the tree as well as might be anticipated. For example, in adult

males the mesosternum in the primitive condition is divided by a ridge. The derived state occurs in the advanced groups of the margarodids and in the higher Neococcoidea. The loss of a ridge apparently developed independently on two different lineages and its reappearance in the Coccidae is yet another independent development.

Discussion. The past use of primitive character states as group criteria, particularly for the Archeococcoidea, has caused a basic misinterpretation of the structure of the basal portion of the phylogenetic tree of the Coccoidea. The Neococcoidea encompass several taxa previously believed to be part of the Archeococcoidea.

Classification of the margarodid groups could be expressed in several ways. An interesting alternative to the classification consisting of the single family Margarodidae would be to treat the Laurasian distribution group (Xylococcini, Neosteingelia, Kuwania, Steingelinae, Matsucoccus, and Margarodinae) as one family, and the Gondwanaland distribution group (Monophlebinae, Coelostomida, and Ultracoelostoma) as a second family. The placement of both Callipappus and the remnants of the Coelostomida is a problem in this scheme, but the approach as suggested by FERRIS (1957) merits further research.

Without the use of PHYSYS, it would have been impossible for me to analyze such a large data set especially with the many complex, multistate character sequences. Use of PHYSYS will be especially helpful in the process of reevaluating the characters as they fit on the tree. PHYSYS and the Wagner algorithm are powerful and effective tools for research on the phylogeny and classification of scale insects and should be used more widely.

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