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# RECENT ADVANCES IN THE STUDY OF SCALE INSECTS[1]

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## INTRODUCTION[2]

Scale insects[3] are some of the most fascinating and unusual organisms in the Insecta. Their unconventional approach to the plant parasitic regime has produced a myriad of bizarre adaptations. As paurometabolous insects, male scales independently have evolved an anomalous complete metamorphosis, which in advanced coccoids includes a unique, second pupal stage. As members of the four-winged Homoptera, male scales are unusual in having the metathoracic wings consistently reduced to stubs (hamulohalteres), and normally only the mesothoracic wings are well developed. Conversely, as reproductively mature nymphs (neotenic), adult females are wingless and in essence are integumental sacks that function as reproductive factories. Other interesting characteristics, elaborated later, include features of sperm, chromosome behavior, hermaphroditism, parthenogenesis, secondary chemicals, including waxes and pigments, endosymbionts, and phylogeny.

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[2]The survey of literature pertaining to this review was completed in January 1978.

[3]The terms scales, scale insects, and coccoids refer to all members of the Coccoidea. Coccid refers only to the family Coccidae, soft scales.

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by the natives of Mexico and Central America as a lacquerlike coating for waterproofing wood and gourds (65). It also has been used as a base for medicines and cosmetic paints. In 1966–1968 the insect was still being cultivated. Scales also are potential biological control agents of noxious weeds. Introduction of *Dactylopius opuntiae* to Santa Cruz Island, California, has nearly eliminated the *Opuntia* cacti that once covered much of the island (52).

## ECOLOGY

The dearth of detailed studies on the ecology of scale insects generally relates to pest species in disturbed habitats. The general lack of ecological studies involving natural systems is surprising, because scale insects have characteristics that offer ample substance for ecological investigations. Coccoids generally are sedentary, allowing for easy censusing, even in heavy populations. After death, several scale families leave covers, ovisacs, or other evidence of their past presence, allowing for gathering of mortality data. Scale insects are readily cultured, they demonstrate an array of host-scale interaction, they have a diverse complex of natural enemies, they maintain mutualistic relationships of various intensities with both plants and animals, they occur in most terrestrial habitats having plant life, they are involved in competitive interaction, they occur on nearly all parts of the host, and the females are always apterous and males may be macropterous, brachypterous, or apterous.

### *Host-Scale Interaction*

The interactions of scale insects with their host plants are complex and suggest many intriguing questions. Host plants often show varying degrees of susceptibility to a particular scale insect. For example, *Citrus* may be heavily infested by a particular coccoid in one area, whereas it may be immune to attack in another area (31). It is not uncommon to find a heavy infestation on one of two plants of the same species growing side by side and a light infestation on the other plant. Likewise, a plant may be susceptible to scale infestation one year and immune the next. Occasionally, a coccoid species that normally remains in small numbers may have sporadic outbreaks. Flanders (49) attempted to explain these phenomena. He suggested that some plants are genetically immune and never susceptible, some fluctuate from immune to susceptible, and some are always susceptible. The plants in the middle category have "pheno-immunity," i.e. an environmentally induced, physiological resistance to a particular coccoid. Flanders presented evidence supporting his hypothesis that meteorological changes

elongation in *Pinus contorta* and *Pinus jeffreyi* affected the location of crawler settling sites of *Chionaspis pinifoliae.* This resulted in divergent crawler mortality on the different host species. *Chionaspis nyssae* has a different life history on the stems and leaves (72). In the fall, adult females on leaves continue to lay eggs until leaf-fall and ultimately die, whereas on stems they do not lay eggs until the following spring. Similar host-related influences on scale phenology probably pervade the Coccoidea.

The effect of the host on coccoid morphology has attracted the interest of systematists since the early part of this century. Soft scales were demonstrated to assume divergent morphologies on different hosts (41, 88). Armored scale species have been shown to have such different leaf and stem forms that they have been treated as separate species and even separate genera (72, 84, 138, 139, 146). The factors affecting this change have not been investigated, but the development of stem forms on senescing leaves and intermediate forms on petioles (72) suggests that the casual factors are differences in the chemical nature or physiology of parts of the host plant. Danzig (34) hypothesized that nutritional differences in the sap of leaves and stems causes dimorphism.

Recent biological studies indicate that hosts may have a profound influence on the speciation of some scales. The obscure scale *Melanaspis obscura* was suggested to be two sympatric, sibling species (142) that have remarkably different life histories. The species that infests white oak (white oak group) overwinters as settled crawlers and is about 1 month later in its life history than the species on pin oak (red oak group) that overwinters as second instars. Timing of male development prevents interbreeding. Oaks in the white and red groups differ in their phenology; those in the former develop mature fruit in 1 year and those in the latter require 2. These closely related sibling species probably evolved through divergent adaptation in response to different host phenologies. A similar situation occurs in *Chionaspis pinifoliae* (82, 83). On *Pinus contorta* this insect overwinters as eggs, whereas on *Pinus jeffreyi* overwintering occurs principally as gravid females. Noticeable differences are apparent in host phenology, particularly in needle development. These differences, combined with the unisexual nature of one form, suggest that the scales are reproductively isolated. Sufficient differences in life history and parasite complexes prompted Rosen & DeBach (122) to suggest that "there is a strong case for recognizing the two 'ectotypes' of the pine needle scale as distinct sibling species."

A study by Rieux (119) develops an additional hypothesis relating to host influence on scale speciation. Because species of *Matsucoccus* are restricted to specific groups of *Pinus,* Rieux concluded that such trophic affinities are probably the result of concomitant speciation within *Pinus* and *Matsucoccus.*

ent populations that otherwise would escape conventional survey techniques (132). Male-trapping information may serve as baseline data for scale control in integrated pest management programs (121, 154) by enabling entomologists to predict the abundance and time of appearance of various pest species. Traps could be used to capture and destroy sufficient numbers of adult males to suppress population growth. Synthetic pheromones could be dispensed in such quantities as to cause mating disruption. These techniques are effective components of the control programs of other insect pests (12).

## *Kairomones*

Several studies indicate the presence of chemicals associated with scales that have kairomonal activity. A high-molecular-weight component of the hemolymph of *Coccus hesperidum* plays an important role in the host selection-oviposition behavior of the hyperparasite *Cheiloneurus noxius* (160). Water extracts of the scale covers of early adult females of *Aonidiella aurantii* solicit oviposition-related behavior in a primary parasite *Aphytis* sp. (116). Kairomonal attraction of the parasite *Arhopoideus peregrinus* by *Planococcus citri* and *Pseudococcus calceolariae* is suggested by pheromone trapping data taken in citrus groves in Italy (126). Similar trapping data support the hypothesis that a chemical associated with *A. aurantii* elicits a kairomonal response in *Aphytis* parasites (48, 140). The use of kairomones in the manipulation of natural enemies shows merit in biological control and integrated pest management programs (67, 155) and warrants scrutiny relative to scale insect control.

## *Insect Growth Regulators*

Insect growth regulators (IGR) that have juvenile hormone activity show great promise as effective control agents of scale insects (54, 100, 136). Depending on the chemical and the quantity used, IGR may cause direct mortality (137) or affect molting, fecundity, egg development (136), and sex pheromone production (100). Most chemicals have divergent effects on males and females (100) and often are more disruptive to males (13, 157). In tests with one IGR, male mealybugs produced extra pupal stages that had a mixture of adult and pupal characters and had coincidental regressive morphogenesis (158). Susceptibility of scales varies with the chemical composition of the IGR and the species. One developmental stage may be considerably more sensitive than others (131, 135), or stages may be equally vulnerable (157). The IGR kinoprene is marketed commercially and is effective against soft scales and mealybugs, but it is currently too expensive to manufacture to be competitive with other scalicides (J. A. Davidson, personal communication). Because IGR are reasonably specific, have low

# GENETICS[4]

## *Chromosome Systems*

Coccoid chromosomes lack localized centromeres and undergo an inversed meiotic sequence in relation to reductional and equational divisions (26). The Coccoidea contain an array of chromosome systems apparently reflecting the diversity of adaptive specialization (24). Nine different sexual chromosome systems exist (29), although several are minor modifications of other systems and are not discussed here. The systems are XX female—XO male, 2N female—2N male, and 2N female—N male, which includes hermaphroditism, and the lecanoid, comstockiella, and diaspidoid systems.

In the XX—XO (27, 60) and 2N female—2N male systems (20), spermatogenesis involves two divisions, and each primary spermatocyte develops into four sperm. Chromosome behavior is normal, except the 2N males lack chiasmata. Maternal and paternal chromosomes are present in the sperm.

In the haploid male system spermatogenesis involves an equational division only, and each primary spermatocyte develops into two sperm (61). Because males are haploid and are formed from unfertilized eggs, sperm contain chromosomes of maternal origin only. Hermaphroditism is known in five species of margarodids in the genus *Icerya,* including the cottonycushion scale *Icerya purchasi* (24, 62). Development of the ovotestis is initiated by haploidization of individual nuclei of the early first-instar gonad (61, 62). Some nuclei become bilobed, with each lobe containing a complete haploid set (24). The chromosomes in one lobe of each nucleus degenerate with the resultant formation of a haploid nucleus. The haploid nuclei proliferate rapidly, forming spermatogenic masses (62). Chromosome behavior is the same as in the 2N—N system, except it is not known whether sperm chromosomes are of maternal or paternal origin (24).

The lecanoid system differs radically and involves the occurrence of a normal (euchromatic) haploid set and a deeply pigmented or heavily condensed (heterochromatic) set of chromosomes in male embryos and in most male tissues. Heterochromatic chromosomes are of paternal origin and are genetically inactive (28). During spermatogenesis two divisions occur and a quadrinucleate spermatid is formed, but the nuclei containing the heterochromatic chromosomes degenerate and only the two nuclei with euchromatic sets form sperm (29, 60). Because the heterochromatic chromosomes are of paternal origin only and are eventually eliminated in spermatogenesis, males act as true haploids, transmitting chromosomes of maternal origin only (28, 70).

[4]Since this manuscript was completed, a detailed treatment of certain aspects of scale chromosome behavior has been published (25a).

Nur (109, 111, 112) discussed the ramifications of parthenogenesis and the variable occurrence of males relative to chromosome systems and homozygosity.

### *Polyploid Tissues*

Mycetocytes and mycetomes are frequently polyploid and therefore the formation of these unusual structures has been of considerable interest to geneticists. As with most coccoid characteristics, the origins of endosymbiont organs are diverse. They may develop from zygotic nuclei, maternal nuclei, polar bodies, polar bodies plus zygotic nuclei, or maternal mycetocytes that fuse with a zygotic nucleus (U. Nur, personal communication) (30, 150, 153). Other scale tissues are polyploid, for example the malpighian tubules of *Planococcus citri* (110).

## ENDOSYMBIONTS

Coccoid endosymbionts exhibit extraordinary diversity. These organisms may be bacteroids or yeastlike and occur in specialized cells (mycetocytes), in specialized organs (mycetomes), in fat tissues, in fat cells, in enlarged midgut cells, or free in the hemolymph. They may be transmitted to the oocytes by any of several complicated methods. Some taxa have a single symbiont type; others have two (30).

These organisms occur widely, but sporadically, in the Coccoidea; their absence apparently has developed through degenerative loss (30). Insufficient information is available on the quality of the plant sap ingested by scales to propose a definitive hypothesis for the presence or absence of coccoid endosymbionts. However, existing data suggest that symbionts supply certain essential vitamins and amino acids unavailable elsewhere (47). Symbionts apparently synthesize nitrogenous products by fixing nitrogen supplied through the tracheal system and by breaking down excretory nitrogenous compounds (47, 149). Buchner (30) hypothesized that scale groups lacking symbionts either obtain a complete diet from their host by feeding in parenchyma cells rather than in phloem sieve tubes, or, in an exceptional case, receive critical nutritional supplements from ants.

Transferral of endosymbionts from generation to generation is implemented transovarially (30). Usually symbionts penetrate the developing oocytes alone, but in *Macrocerococcus superbus* entire mycetocytes are transferred. These maternal cells are polyploid when transmitted and continue to increase their chromosome number endomitotically to form giant polyploid cells. Eventually these cells undergo unusual somatic reduction, giving rise to transmission mycetocytes (151). The most remarkable aspect

## *Taxonomic Characters*

Historically, scale classification has been based almost exclusively on the morphology of adult females. Pragmatically, this has been a reasonable approach because this instar is commonly encountered and is nearly always available. The resultant classification is a basis for future holistic studies, but the relative paucity of distinguishing features on the degenerate female has caused problems. At the familial level the scheme based on analysis of females is generally consistent with information derived from other sources, especially from adult males (15). However, serious discrepancies in classification are manifested at the generic level. For example, Morrison (104) included two fossorial genera in his revision of the Margarodidae, and although descriptions of adult males and immatures were included, his generic concepts were based primarily on adult females. Over a period of 19 years Jakubski (64) studied available material of all instars of these "genera" and concluded that the fossorial group should be distributed among two families, five subfamilies, seven tribes, and 10 genera. The ranking of these subdivisions is open to controversy, but it is quite clear that adult female morphology led to a poor interpretation of fossorial margarodid classification. Similar, though less drastic, examples have been found in mealybugs (95) and armored scales (143) and probably pervade the Coccoidea. Scales from widely different lineages appear to have invaded similar habitats and developed convergent morphologies (95). Adult males and first instars seem to be most useful in clarifying convergences, because they are least affected by host plant changes (97).

Beginning with the detailed works of Ferris (46), Morrison (103, 104), and Balachowsky (4), external morphological features of adult females have been of paramount importance in coccoid taxa discrimination. Useful characters include the distribution and kinds of wax pores, the relative development of appendages, and the arrangement and types of setae. Recent studies have shown that structural details of the generally ignored labium (76), clypeolabral shield (79), and tarsal campaniform sensilla (75) are important taxonomic characters.

Internal structures largely have been ignored by scale systematists, but recent work shows that differences in the salivary pump may be useful in segregating taxa (78). Nur (108) has demonstrated the taxonomic utility of the spermatheca relative to other reproductive organs. Many more internal taxonomic characters probably await discovery.

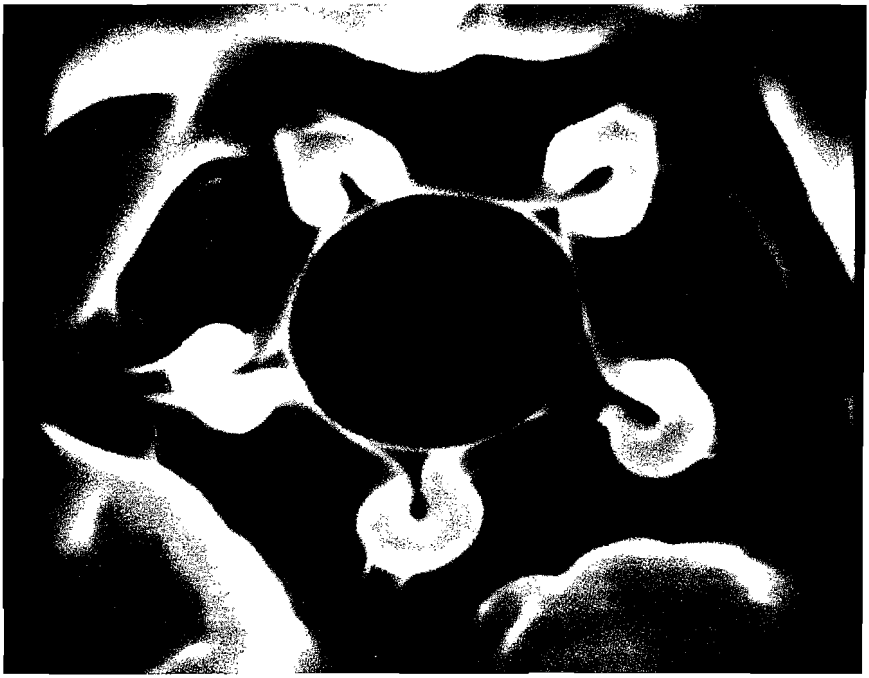
Unlike neotenic adult females, adult males are fully mature insects and as such are especially appropriate for systematic analysis. Unfortunately adult males are ephemeral and usually live from a few hours to a day. Because specimens are difficult to obtain, such males largely have been ignored by scale systematists. However, recent works of Boratynski (14, 15),

end piece (38, 39, 85, 108). Ultrastructural comparisons of the bundles also may warrant consideration (120). Taxonomic differences occur in details of the configuration and numbers of sperm within each bundle and of the arrangement and numbers of microtubules in each sperm. Robison (120) found 32 and 16 sperm, respectively, in each bundle of *Melanaspis smilacis* and *Melanaspis tenebriocosa.* Based on the limited data available, it appears that bundle sheath morphology and microtubule numbers will be useful in separating lower category taxa, whereas other sperm features will find application at higher levels.

Coccoid endosymbionts are bacteroids or yeastlike and are stored in various tissues (152). Buchner (30) demonstrated the relatively incongruous occurrence of these organisms. Although it is not unusual for more than one endosymbiont to coexist in a single scale, competitive replacement apparently occurs (30), and degenerative loss is reported in widely separated lineages (152). Therefore the phylogeneticist should look elsewhere for useful data. On the other hand, endosymbionts seem replete with features of diagnostic value. Differences in the kinds of organisms, the embryological methods of generation transferral, and the kinds of endosymbiont storage tissues are useful characters. Endosymbiont differences in closely related species of *Lecanium* have been demonstrated (112).

The sequence of coccoid chromosome systems appear to provide one of the most important clues to the evolutionary history of scales. Although Brown (24) showed that chromosome behavioral changes occur after selective transformation into a new adaptive zone, chromosome systems apparently closely reflect many of the major transformations. Chromosome numbers have been examined in detail in the armored scales (22), eriococcids (23), and to a limited extent in other groups (60, 111). In general these numbers are similar in closely related lower taxa but differ among higher taxa. An exception is reported in two similar species of *Protodiaspis* that have haploid numbers of three and four, respectively (93). The relative abundance of chromosomes generally is unrelated to ancestral history. Brown (22) explains this apparent inconsistency by the relative ease with which scales are able to maintain fractured or fused chromosomes.

The relevance of parasites as sources of systematic information in scale classification has recently been summarized (122). Differences in parasite-scale associations frequently have been the initial stimulus leading to the discovery of two closely related coccoid species. In some instances the presence of a single parasite may be sufficient evidence for diagnosis, but generally data on the composition and relative abundance of the parasites within the complex are needed for coccoid determination. Surprisingly, higher category correlation is found in the virtual absence of wasp parasites in the Archeococcoidea and their abundance in the Neococcoidea. Other associations are reported, particularly in family-genus taxa.



these fossils is controversial (44). *Mesococcus asiatica* is an impression of an adult female or immature from Upper Triassic deposits of the USSR. Although it is considered a scale, Beardsley (10) points out that not enough diagnostic coccoid features are preserved to be reasonably certain of its superfamilial identity. An adult male of *Electrococcus canadensis* from Upper Cretaceous amber represents an extinct margarodid genus. The possession of 10 unicorneal eyes places it as an annectent Archeococcoidea-Neococcoidea group showing a considerable degree of specialization. Although useful fossil evidence is scarce, it seems likely that the Coccoidea diverged from the aphidoid sister group sometime in Early to Middle Permian (144). The high degree of specialization of *Electrococcus* and the apparent small amount of divergence since Oligocene and Miocene times suggest that primary coccoid radiation occurred before the end of the Mesozoic.

Coccoidea phylogeny has attracted only a modicum of interest, although a relatively clear ancestral sequence persists in the extant fauna. Phylogenetic assessments of familial categories have been stated briefly by Borchsenius (16), Boratynski & Davies (15), and Koteja (77) and are based on characteristics of adult females, adult males, and adult female mouthparts, respectively. General agreement is found among these analyses, although the greater number of family group taxa in Koteja's analysis cause it to appear to be different. In the arrangements of Borchsenius and Boratynski & Davies, the Archeococcoidea (margarodoids) are considered most primitive, the mealybugs, eriococcids, soft scales, pit scales, and associated families (lecanoids) are more advanced, and the armored scales (diaspidoids) are the most advanced. Boratynski & Davies, unlike Borchsenius, suggested that the lecanoid group is polyphyletic, having a mealybug-eriococcid lineage and a soft scale-pit scale lineage. Brown (24) agreed with this hypothesis, although he apparently considered the eriococcids to be part of the soft scale lineage, unassociated with the mealybugs. Koteja's arrangement takes into account the great amount of specialization that has taken place within the primitive margarodoid groups.

Since a detailed cladistic analysis has yet to be undertaken, a modified version of the more traditional phylogram by Boratynski & Davies (15) is given as a basis for further discussion (Figure 2). Gradual specialization seems to be the trend within the Coccoidea. A brief synopsis of major evolutionary sequences is given as follows.

As scales have become more highly specialized, their mobility has decreased. Primitive families tend to be quite mobile and have large, well-developed legs with numerous setae. The mealybug-margarodoid annectent genus *Puto* retains this mobility (159), but mealybugs tend to have smaller legs with fewer setae and probably are less mobile. Other lecanoid groups

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