REVIEW ARTICLE

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Coccidology. The study of scale insects (Hemiptera: Sternorrhyncha: Coccoidea)

Coccidología. El estudio de insectos escama (Hemiptera: Sternorrhyncha: Coccoidea)

RESUMEN

Se presenta una breve introducción a la ciencia de la coccidología y se discute una sinopsis de la historia, avances y desafíos de este campo de estudio. Se hace una breve revisión de los cambios de la coccidología desde la publicación de *Systema Naturae* por Carolus Linnaeus hace 250 años. También se discuten la importancia económica, las relaciones filogenéticas y la aplicación de códigos de barras del ADN en la identificación de insectos escama.

Palabras clave: insectos, escama, coccidae, ADN, historia.

ABSTRACT

A brief introduction to the science of coccidology, and a synopsis of the history, advances and challenges in this field of study are discussed. The changes in coccidology since the publication of the *Systema Naturae* by Carolus Linnaeus 250 years ago are briefly reviewed. The economic importance, the phylogenetic relationships and the application of DNA barcoding to scale insect identification are also considered in the discussion section.

Keywords: Scale, insects, coccidae, DNA, history.

INTRODUCTION

Coccidology is the branch of entomology that deals with the study of hemipterous insects of the superfamily Coccoidea, particularly on areas related to systematics. For the purpose of this synopsis, we set the starting point for the study of coccidology as 1758, beginning with Carl Linnaeus' 10th edition of the *Systema Naturae* (Linnaeus, 1758). During this period of 250 years, the number of described scale insects has increased from 24 species (Williams, 2007) to some 7,700 species in more than 1,050 genera (Ben-Dov *et al*., 2006). The root of the word coccidology is derived from the word "*Coccus*", the genus in which Linnaeus included the bulk of his scale insects. Most scale insects were not recognisable as insects by the ancients, but rather as seeds or berries, and were given the ancient Greek word "Kokkos" and then the later Latin word "Coccus" meaning a berry. The word "coccidology", as a branch of entomology, was probably coined for the first time by Tinsley (1899) in his article "Contributions to coccidology. I." Here we attempt to summarize briefly how coccidology has changed in the last 250 years, with emphasis on the remarkable changes that have happened in the field in the XXI century. This account supplements a brief history of Coccoidea by Ferris (1957).

What are scale insects?

Scale insects are sap sucking hemipterous insects that include all members of the superfamily Coccoidea. These are closely related to aphids (Aphidoidea), whiteflies (Aleyrodoidea) and jumping plant lice (Psylloidea), which make up the suborder Sternorrhyncha (Gullan & Martin, 2003). These insects are usually less than 5 mm in length. Their taxonomy is based mainly on the microscopic cuticular features of the adult female. The adult female is paedomorphic, maturing in a juvenile form, whereas the adult male (when present), after going through a prepupal and pupal stage, turns into an alate with non-functional mouthparts. The Coccoidea form a rather small group of insects in terms of species richness with some 7,700 species described. However, scale insects are an interesting group of insects to study. According to Gullan & Cook (2007), scale insects have great variation in chromosome number (Nur *et al*., 1987); sperm structure (Robison, 1977; 1990); types of bacterial endosymbioses (Buchner, 1965; Thao *et al*., 2002; Gruwell *et al*., 2005, 2007); and genetic systems, including hermaphroditism, diplodiploidy, thelytoky and haplodiploidy (Nur, 1980; Normark, 2003). Their morphology varies greatly amongst members of the different families, with some species producing cysts (e.g. Margarodidae *sensu stricto*) that can live underground for many years, and other species are highly modified to live under the bark of their hosts (e.g., some Diaspididae and Eriococcidae). For ecologists and evolutionary biologists, scale insects are often subjects to study because of their mutualistic relationships with tending ants and their close associations with their hosts. For example, the ant-scale association in *Macaranga* plants has been a subject of studies in Southeast Asia (Heckroth *et al*. 1998; Ueda *et al*., 2008). Moreover, some scale insects are even known to have symbiotic relationships with stingless bees (Hymenoptera: Apidae: Meliponinae) (Camargo & Pedro, 2002).

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There are currently 46 known scale insect families, of which 32 are extant and 14 are known only as fossils. Scale insects are generally divided into two informal groups, the archaeococcoids and the neococcoids. The archaeococcoids are defined by the presence of 2–8 pairs of abdominal spiracles, which are absent in the neococcoids. The archaeococcoids consist of 27 families, i.e., 15 extant families (Callipappidae, Carayonemidae, Coelostomidiidae, Kuwaniidae, Marchalinidae, Margarodidae, Matsucoccidae, Monophlebidae, Ortheziidae, Phenacoleachiidae, Pityococcidae, Putoidae, Steingeliidae, Stigmacoccidae and Xylococcidae) and 12 fossil families (Electrococcidae, Jersicoccidae, Kukaspididae, Labiococcidae, Naibiidae and seven recently described families, namely Arnoldidae, Lithuanicoccidae, Weitschatidae, Grohnidae, Serafinidae (Koteja, 2008), and Hammanococcidae and Lebanococcidae (Koteja & Azar, 2008)).

The neococcoids are composed of 17 extant families, i.e., Aclerdidae, Asterolecaniidae, Beesoniidae, Cerococcidae, Coccidae, Conchaspididae, Dactylopiidae, Diaspididae, Eriococcidae, Halimococcidae, Kermesidae, Kerriidae, Lecanodiaspididae, Micrococcidae, Phoenicococcidae, Pseudococcidae and Stictococcidae; and 2 extinct families, namely Inkaidae and the recently described Pennygullaniidae (Koteja & Azar, 2008). Koteja and Azar (2008) considered the Putoidae a neococcoid, however, we consider this family (and the probably related Labiococcidae) to belong to the archaecoccoids. The adult females of species of Putoidae superficially are most similar to those of the neococcoid family Pseudococcidae, with most females of these families possessing trilocular pores, cerarii and dorsal ostioles. However, the adult females of Putoidae differ from those of Pseudococcidae in having: (i) three or four campaniform sensilla on each surface of each trochanter; (ii) three pairs of interflagellar setae; and (iii) a pair of basal denticles on each claw (Hardy *et al*., 2008). Furthermore, the adult males of putoids differ from those of pseudococcids in many morphological features (Hardy *et al*., 2008; Hodgson & Foldi, 2006) and the chromosome system of putoids does not show paternal genome elimination, which is characteristic of neococcoids (Cook *et al*., 2002).

Scale insects are known by various names depending on the family to which they belong, e.g., the armoured scales (Diaspididae), the mealybugs (Pseudococcidae), the putoids (Putoidae), the soft scales (Coccidae), the felt scales (Eriococcidae), ground pearls (Margarodidae), lac insects (Kerriidae), cochineal insects (Dactylopiidae), and ensign scales (Ortheziidae). The most commonly encountered families are those with the most species, namely the Diaspididae, Pseudococcidae and Coccidae.

Although among the ortheziids *Arctorthezia cataphracta* (Olafsen) is known to feed on a basidiomycete fungal species (Thorpe, 1968) and *Newsteadia kanayana* Kawai & Takagi on fungal mats (Kawai, 1980), the majority of scale insects feed on plants, especially flowering plants (angiosperms). Scale insects are generally phloem-sap feeders; however, some feed on parenchyma tissue by directly feeding on the contents of parenchymatic cells. Scales are found on various parts of their hosts, and may infest leaves, twigs, branches and roots, and some live inside plant domatia. Some scale insects are even known to survive on plants completely submerged at high tide (Harrison, 1916). Many are important pests of agriculture (e.g., Peronti *et al*., 2001; Miller *et al*., 2005; Culik *et al*., 2007) and may injure or kill plants by depleting them of their sap, injecting toxins, transmitting viruses or excreting honeydew, which serves as a medium for sooty moulds (Williams & Granara de Willink, 1992; Gullan & Martin, 2003).

Scale insects have been known for centuries, not just for the damage they cause, but for the useful red dyes that some of them produce, for valuable secretions in the form of waxes and resins, and even for their use as medicine and food. In the Oriental Region, Mahdihassan (1954), for instance, has given us an account of how lac insects were known to the Chinese in writings dating to 320 AD when the insects produced a red dye and a substance for sticking things together. Lac insects are now known to be tropicopolitan. The most important species are still deliberately grown in India and surrounding countries for shellac and sealing wax. The use of lac in India probably dates back many centuries. In the New World, Chamberlin (1923) reported that the Mexicans used the lac of *Tachardiella fulgens* Comstock, under the name of "jomilla", medicinally and for repairing crockery and other utensils. Kamel & Afifi (1970) have reported how the wax from *Ceroplastes africanus* Green in Egypt is used for welding porcelain and mending metal cracks and holes.

Another scale insect, *Kermes vermilio* Planchon (Kermesidae), that produces a red dye, has been known for more than two millennia and lives on species of oaks around the Mediterranean shores (Foldi, 2003). These insects were originally thought to be little worms, hence the Latin name *vermiculi* from which the name vermilion is derived (and similar names in languages derived from Latin).

Armenian red, a name for the red dye obtained from the scale insect *Porphyrophora hameli* Brandt that lives mainly on grass roots in Armenia and surrounding countries was widely used for dying silks (Donkin, 1977b). A related insect *Porphyrophora polonica* (L.) found in Poland and surrounding areas, known as the Polish cochineal insect, also feeding on roots, was widely used to produce a red dye and exported to Western Europe. Both of these insects are peculiar in that the intermediate instars encyst and these cysts were originally thought to be of plant origin. A famous treatise on this insect by John Philip Breyn (Breyn, 1731) showed how an insect could be studied in detail and illustrated showing all the instars.

In the New World, the cochineal insect of commerce, *Dactylopius coccus* Costa, a species used by Mayans, Aztecs and Incas, interested many European workers. The red dye produced by this insect proved to be superior to any of the red dyes produced by other scale insects (for an account see Donkin, 1977a) and at a time the species was even grown on cactus in North Africa. The Spanish also exported supplies to southern Asia via the Philippines from South America (Donkin, 1977b). Currently, the cochineal insect is grown for commercial purposes in Chile, Mexico, Peru and the Canary Islands. Cochineal dye is still produced commercially in chemical factories in Europe and the USA (Pérez Guerra & Kosztarab, 1992) and has been used as a biological control agent of noxious *Opuntia* weeds (Moran & Zimmermann, 1984; Volchansky *et al.*, 1999).

Scale insects provide other products too. It is generally thought that flower nectar is the main ingredient of honey. However, honeybees collect other sweet ingredients, especially when flowers are scarce. In Greece and Turkey, honeybees collect honeydew from *Marchalina hellenica* (Gennadius) (Marchalinidae) feeding on pine trees and, in Greece alone, this "pine honey" accounts for 60%–65% of all honey produced (Hodgson & Gounari, 2006). In Middle Europe, about 50% of all honey produced is from honeydew, particularly from the soft scale *Physokermes hemicryphus* (Dalman), a species found mostly on the Norway spruce, *Picea abies* (Kunkel, 1997). According to Kunkel (1997), the honeydew of many species of scale insects in at least six families are known as a source of bee honey worldwide.

The pela wax scale, *Ericerus pela* (Chavannes), is cultivated in China for the production of high quality wax (Qin, 1997). The wax of this soft scale is produced by the immature stages (second-instar nymphs, prepupa and pupae) of the males and is used for making candles, coating material for pills, papers, and for shining leather products and tires amongst its uses.

Some scale insects are also used as human food. In Australia, aboriginal people eat the gall-inducing scale, *Cystococcus pomiformis* (Froggatt), which according to the natives has a watery female and nutty-flavoured nymphs (Gullan & Cranston, 2005). In Sakorn Nakorn Province, Thailand, the giant mealybug, *Nietnera* sp. (Margarodidae *sensu lato*) is cooked together with sticky rice and consumed (Kondo, 2001).

History of Coccidology

Like many other fields in entomology, coccidology has gone through its own evolution. The original Latin description of *Coccus hesperidum* (L.), as given in *Systema Naturae* (1758: 455-457) can be fitted in one sentence as follows: "The Coccus of the greenhouses; It lives on evergreen trees" (English translation as given in Williams, 2007). The most recent redescription of *C. hesperidum* by Hodgson (1994) consists of three and a half pages beginning with a section on classification and nomenclature, a description including the morphology of the insect in life and of slide-mounted specimens as seen under a compound microscope, a figure, a section on the material studied and a discussion section where the author considers its affinities with other coccids. In Linnaeus' time, a single sentence sufficed to describe *C. hesperidum*, however, the family Coccidae in which *C. hesperidum* is included currently contains more than 1,100 species in more than 100 genera! Even after 250 years, *C. hesperidum* continues to be a common scale insect in greenhouses, but we know now that there are many other scale insects that are commonly found in greenhouses. For example, in southeastern USA, according to Baker (1994), the list of common scale insects in greenhouses and on indoor plants includes the mealybugs: *Planococcus citri* (Risso), *Pseudococcus longispinus* (Targioni Tozzetti), *Phenacoccus gossypii* Townsend & Cockerell [probably a misidentification of *Ph. madeirensis* Green], *Rhizoecus falcifer* Kunckel d'Herculais, the armoured scales *Diaspis boisduvalii* Signoret and *Pinnaspis aspidistrae* (Signoret), and the soft scales, *Coccus hesperidum* L., *Eucalymnatus tessellatus* (Signoret) and *Saissetia coffeae* (Walker). Thus, Linnaeus's 1758 description of *C. hesperidum* is not useful in the present day.

It was René Antoine Ferchault de Réaumur who produced a remarkable account of scale insects, mainly of Europe, with illustrations of the external appearance (Réaumur, 1738), many of which can be recognised today. Linnaeus (1758), in his *Systema Naturae*, the starting point of zoological nomenclature, drew heavily on Réaumur's work for his chapter on the genus *Coccus*.

In the 18th and 19th centuries, some of the European countries were interested in the fauna of their overseas territories. Insects were sent to Europe for identification and it became clear that identification from the external appearance was not satisfactory. With better microscopes, entomologists such as Signoret in many works on scale insects from 1860–1886 produced articles based on slide-mounted specimens (Ben-Dov & Matile-Ferrero, 1995). Unfortunately, only a few of his mica slides have survived (Deyrolle, 1875).

There then followed important works based on slide-mounted specimens by William Miles Maskell in New Zealand from 1879–1897 and by Theodore Dru Alison Cockerell, Edward Ernest Green, Robert Newstead and many French workers whose slide collections are housed in the United States National Museum of Natural History (actually at the USDA, Beltsville, Maryland), The Natural History Museum, London, and the Muséum National d'Histoire Naturelle, Paris. Although identifications are possible from many illustrations by these authors, we owe much gratitude to Gordon Floyd Ferris who, in a series of articles published in the journal Microentomology from 1936–1955 and in his Atlas of Scale Insects of North America (1937–1955), adopted a method of illustration first used by Karl Šulc (Šulc, 1895). This method includes a full outline of the insect divided by a line in the middle and showing the dorsum on the left and the venter on the right with enlargements of important characters either elsewhere on the illustration or around the perimeter of the main drawing. This unique drawing method for scale insects was adopted later by Alfred Serge Balachowsky and most subsequent authors and has stood the test of time so that accurate identifications can now be made from printed works. Although access to slide collections is necessary, it has even become clear that some of the oldest microscope slide preparations in collections can be remounted successfully when necessary.

Scale insects as economic pests

There have probably been outbreaks of scale insects causing damage to local crops and plants for centuries, but the arrival in the USA of *Icerya purchasi* Maskell (Monophlebidae) towards the end of the 19th century, resulting in the almost collapse of the citrus industry, seemed to attract attention throughout the world. Outbreaks causing considerable damage are occurring to the present day and in the last 40 years the accidental introduction of the cassava mealybug *Phenacoccus manihoti* Matile-Ferrero (Pseudococcidae) from South America to

West Africa caused considerable damage to cassava throughout Africa affecting the staple food of 200 million people (Herren & Neuenschwander, 1991). About the same time, another mealybug *Rastrococcus invadens* Williams was introduced to West Africa from the Oriental Region affecting a wide variety of fruit trees (Agounké *et al*., 1988). In more recent times, the hibiscus mealybug *Maconellicoccus hirsutus* (Green) was introduced accidentally to the Caribbean area affecting a large number of plant species including fruit trees and plants of economic importance (Chang & Miller, 1996). Yet another mealybug species, the papaya mealybug *Paracoccus marginatus* Williams & Granara de Willink that had been known only locally in Mexico, suddenly spread to much of the Caribbean area and beyond (Miller *et al*., 2001). All of these pest species were brought under control by parasitoids or predators with the aid of taxonomists who could identify the pest species accurately and suggest areas where natural enemies could be located. More recently, the lobate lac scale *Paratachardina pseudolobata* Kondo & Gullan has caused serious damage in Florida, the Bahamas and in Christmas Island, Australia (Kondo & Gullan 2007; Schroer *et al*., 2008). In Florida alone, the lobate lac scale has been recorded on over 300 species of plants (Howard *et al*., 2006). Now this scale has also been reported in Cuba, and no effective natural enemies have been found because its place of origin is still unknown.

One would expect that these outbreaks might lead to an increase in workers studying the group but in three of the world's most important centres for scale insects housed in the USDA at Beltsville, Maryland, The Natural History Museum, London, and the Natural History Museum in Paris, there are no full-time employed incumbents and research is carried out by retired associates or collaborators.

The phylogenetic relationships of scale insects

New tools and resources are making the study of scale insects by taxonomists more exciting, and in some administration centres it is thought that eventually identifications from the DNA of a species could dispense with the skill of the traditional taxonomist. However, there will always be a need to link a DNA sequence to a certain species, which needs to be identified by the traditional taxonomic expert.

The classification of the Coccoidea, particularly the archaeococcids has gone through a series of overhauls in the last 40 years. Koteja (1974) introduced a multi-family classification for scale insects based on the morphology of mouthparts recognizing a number of families formerly included in the Margarodidae *sensu lato*. In a special edition of the online journal Zootaxa celebrating the 300th anniversary of the birth of Carolus Linnaeus (Zhang & Shear, 2007), Gullan & Cook (2007) gave a summary of our current understanding of the higher classification of the Coccoidea. Many coccidologists now accept that the superfamily Coccoidea comprises up to 32 extant families. The neococcoids are considered more derived than the archaeococcoids and form a monophyletic group supported by both morphological and genetic data, but the monophyly of the archaeococcoids is uncertain and their higher-level ranks have been controversial.

Recent studies using the nuclear small subunit ribosomal RNA gene (SSU rRNA or 18S) have helped resolve some of the higher relationships within the Coccoidea, particularly those of the neococcoids. According to Gullan and Cook (2007), future studies may show that some of the species-poor families are autapomorphic members of a larger group, e.g., the Aclerdidae and Micrococcidae are similar to Coccidae and their recognition at family rank may render the Coccidae paraphyletic; the Beesoniidae, Dactylopiidae and Stictococcidae are each closely related to a different subset of the Eriococcidae in molecular phylogenetic studies; the Phoenicococcidae is monotypic and together with the Halimococcidae has affinities to the Diaspididae; the Conchaspididae resemble the diaspidids and also other distantly related neococcoids, and its phylogenetic position is an enigma.

The higher-level relationships of the archaeococcoids still remain unresolved. According to Gullan and Cook (2007), the extent of 18S divergence among the coccoid families is as high as or higher than among the aphid families, and it seems that the radiation of extant archaeococcoid families occurred well prior to that of extant aphid families. They suggest the lack of resolution of relationships among scale insect families from 18S data and morphology indicates that the basal radiations might have been relatively rapid (Gullan & Cook, 2007).

In order to elucidate the unresolved phylogenetic relationships of scale insects, future studies may consider increasing taxon sampling and the number of informative genetic markers, as well as adding more morphological data, especially from the adult males and first-instar nymphs.

Insects of the suborder Sternorrhyncha harbor maternally transmitted bacteria housed in a specialized organ called the bacteriome (von Dohlen *et al*., 2001). Mealybugs have primary and secondary endosymbionts belonging to different subdivisions of the phylum Proteobacteria, although some mealybug species lack secondary endosymbionts (von Dohlen *et al*., 2001; Thao *et al*., 2002). The primary endosymbionts of armoured scale insects belong to a different phylum, the Bacteroidetes, and their phylogeny follows closely that of their scale insect hosts (Gruwell *et al*., 2007). This appears also to be the case in mealybugs in which the mealybug microbial ecology appears strongly correlated with phylogeny (Downie & Gullan, 2005; Hardy *et al*., 2008). Perhaps it may be possible to help elucidate unresolved relationships of scale insects by looking at the relationships of their endosymbionts.

DNA Barcoding and scale insects

DNA barcoding uses a short fragment of the mitochondrial DNA to link an organism to a species (Herbert & Gregory, 2005). The mitochondrial DNA (mtDNA) of eukaryote cells has a relatively fast mutation rate, resulting in significant variance in mtDNA sequences between species but generally small variation within species. The concept of barcoding has been successfully implemented in organisms such as some birds (Hebert *et al*., 2004a), mammals (Borisenko *et al*., 2008), and insects, especially Lepidoptera (e.g., Hebert *et al*., 2004b). The genetic marker of choice for DNA barcoding (sanctioned by the Consortium for the Barcode of Life, CBOL) has been the 5′ region of the CO1 gene, but in scale insects, universal primers fail to amplify the region for any but a few taxa. Instead the D2 region of 28s rDNA is currently being proposed by scale insect workers as a possible marker for barcoding of scale insects. The barcoding method in coccidology is closely associated with the preparation of voucher specimens and the correct identification of the scale insect by taxonomic experts. The aim of barcoding in scale insects is the accurate, economic and fast identification of important pest species. The damage caused by scale insects is said to sum up to billions of dollars in damage and control every year (Kosztarab, 1990). Coccidologists in general agree that DNA barcoding is not a replacement tool for systematics, but rather a tool that can be used for identification of morphologically defined species. We agree with Kipling and Rubinoff (2004) in that an extremely well developed background knowledge of the taxa to be sampled and an *a priori* understanding of sequence variation among populations and individuals are needed in order to use properly the barcoding method.

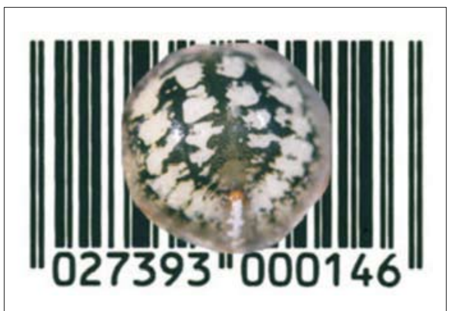

Figure 1. DNA Barcoding and scale insects

DISCUSSION

The advances in coccidology during the last 250 years have been remarkable. The number of scale insect species has increased from 24 species in 1758, to nearly 8000 species today. Our knowledge on the taxonomy of Coccoidea has been substantial; with the advances of high-resolution microscopes, electron microscopy, digital photography, computer illustration and graphic editing programs, molecular biology and phylogenetic methods have contributed to high standard descriptions of scale insects. The worldwide web has made possible the creation of the online scale insect database ScaleNet (Ben-Dov *et al*., 2006), which allows users to obtain information on numerous aspects of most described species by just the click of a button. Advances in molecular genetics are helping to resolve the phylogenetic relationships of this morphologically highly derived group, and new techniques such as barcoding are being contemplated as a tool for identification of common pest species. Despite all of these advances in technology, and our accumulated knowledge about scale insects, the field of coccidology still faces many challenges. The higher-level relationships of scale insects are far from being resolved, and every year there are new species of scale insects being added to the list of agricultural pests. Perhaps, the greatest problem that the field of coccidology faces today is the decline of scale insect specialists worldwide. Museums that used to employ coccidology experts no longer replace the retirees. We only hope that the science of coccidology will continue to progress.

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