



Phylogeny and higher classification of the scale insects (Hemiptera: Sternorrhyncha: Coccoidea)*

P.J. GULLAN¹ AND L.G. COOK²

¹Department of Entomology, University of California, One Shields Avenue, Davis, CA 95616, U.S.A. E-mail: pjgullan@ucdavis.edu

²School of Integrative Biology, The University of Queensland, Brisbane, Queensland 4072, Australia. Email: l.cook@uq.edu.au

*In: Zhang, Z.-Q. & Shear, W.A. (Eds) (2007) Linnaeus Tercentenary: Progress in Invertebrate Taxonomy. *Zootaxa*, 1668, 1–766.

Table of contents

Abstract	413
Introduction	413
A review of archaeococcoid classification and relationships	416
A review of neococcoid classification and relationships	420
Future directions	421
Acknowledgements	422
References	422

Abstract

The superfamily Coccoidea contains nearly 8000 species of plant-feeding hemipterans comprising up to 32 families divided traditionally into two informal groups, the archaeococcoids and the neococcoids. The neococcoids form a monophyletic group supported by both morphological and genetic data. In contrast, the monophyly of the archaeococcoids is uncertain and the higher level ranks within it have been controversial, particularly since the late Professor Jan Koteja introduced his multi-family classification for scale insects in 1974. Recent phylogenetic studies using molecular and morphological data support the recognition of up to 15 extant families of archaeococcoids, including 11 families for the former Margarodidae *sensu lato*, vindicating Koteja's views. Archaeococcoids are represented better in the fossil record than neococcoids, and have an adequate record through the Tertiary and Cretaceous but almost no putative coccoid fossils are known from earlier. In contrast, the sister group of the scale insects (Aphidoidea) has a more informative Jurassic and Triassic record. Relationships among most scale insect families are unresolved in phylogenetic trees based on nuclear DNA sequences, and most nodes in trees based on morphological data, including those from adult males, are poorly supported. Within the neococcoids, the Eriococcidae is not monophyletic and the monophyly of the Coccidae and Diaspididae may be compromised by the current family-level recognition of a few species-poor autapomorphic groups.

Key words: archaeococcoids, neococcoids, systematics

Introduction

Scale insects or coccoids (Coccoidea) are sap-sucking hemipterans with paedomorphic adult females (resembling nymphs), perhaps due to neoteny, and males that display complete metamorphosis (Gullan & Kosztarab,

1997; Gullan & Martin, 2003). Individuals of most scale insect species are small (typically less than 5 mm long) and cryptic in habit, often resembling part of their host plant. Their common name derives from the frequent presence of a protective covering or 'scale' or from the appearance of the insects themselves. Most species produce some sort of waxy secretion that covers the body, either as a structure detached from the body (a scale or test) or as a secretion that adheres to the cuticle. Coccoidea are diverse in terms of chromosome number (Nur *et al.*, 1987), sperm structure (Robison, 1977; 1990), types of bacterial endosymbioses (Buchner, 1965; Gruwell *et al.*, 2005, 2007), and genetic systems, including hermaphroditism, diplodiploidy, thelytoky and haplodiploidy (Nur, 1980; Normark, 2003). Relative to most other insect groups, a high percentage of the estimated 7,700 named scale insect species have been moved around the world by humans and many are important economically as pests of agriculture, horticulture and forestry (e.g. Miller & Davidson, 1990; Miller *et al.*, 2005). Furthermore, there may be many undescribed scale insect species, not just among taxa of poorly studied regions of the world (e.g., one estimate of the species diversity of the Beesoniidae puts it at 50 times the described number (Takagi, 2007)), but also disguised in complexes of morphologically cryptic species. Few scale insects have been examined in enough detail genetically to reveal cryptic diversity, but recent studies suggest that cryptic radiations occur both within relatively well known pest groups (e.g., Gullan *et al.*, 2003) and in scale insects host-specific on radiating host-plant groups (e.g., Cook & Rowell, 2007). If these diversity patterns are more general across scale insect taxa, then undescribed species may well outnumber those described.

The Coccoidea is one of the four superfamilies of the monophyletic suborder Sternorrhyncha within the Hemiptera (Schaefer, 1996; Bourgoïn & Campbell, 2002; Gullan & Martin, 2003). Scale insects are more diverse in terms of major evolutionary lineages (families), species richness, genetic systems and morphology than any of the other sternorrhynchan groups, namely the aphids or aphidoids (Aphidoidea), jumping plant lice (Psylloidea) and whiteflies (Aleyrodoidea). Coccoidea is the undisputed sister group of Aphidoidea (e.g., von Dohlen & Moran, 1995; Sorenson *et al.*, 1995; Bourgoïn & Campbell, 2002). Aphidoid fossils of several extinct families are well documented from as far back as the Jurassic and Triassic (Heie, 1999; Shcherbakov & Wegierek, 1991; Grimaldi & Engel, 2005), but generally only three extant families—Aphididae, Adelgidae and Phylloxeridae—are recognized in recent studies (e.g. Remaudière and Remaudière, 1997; Blackman & Eastop, 2000; von Dohlen & Moran, 2000; Havill *et al.*, 2007). In contrast, scale insects are divided into either 22 (Ben-Dov *et al.*, 2006) or about 30 extant families (Koteja, 1996, 2001a; Miller *et al.*, 2007), and the oldest described coccoid fossils date only from the Early Cretaceous (Koteja, 2001a; Koteja & Azar, 2001; Grimaldi & Engel, 2005), even though the Coccoidea must be as old as its sister group. The fossil record for the scale insects is very incomplete (Grimaldi & Engel, 2005) and Koteja (2001a) explained that scale insects suddenly appear in the fossil record in the Early Cretaceous as an abundant, diverse and specialized group without any "ancestral" forms. He attributed the dearth of pre-Cretaceous fossils to either ecological or preservation conditions, or technical failure to recognize scale insect fossil impressions during sorting. Apparently however, Koteja did recognise two adult male scale insects from the Upper Jurassic (Shcherbakov, 2007), but died before describing them. A recently described extinct family, the Naibiidae, with representatives from the Triassic, Jurassic and Upper Palaeocene, has been ascribed to the coccoid stem group (Shcherbakov, 2007). However, naibiids resemble aphidoids and their phylogenetic position and relationship to the scales insects seem uncertain and may not be settled unless further fossils become available.

Major contemporary issues in scale insect systematics concern the uncertainty of the relationships among scale insect families and the resulting inability to obtain consensus on the rank and names for the higher taxa. Examples include:

- (i) the appropriate rank for some of the species-poor families,
- (ii) how to deal with the non-monophyly of the Eriococcidae within the neococcoids, and
- (iii) the status of the archaeococcoids and Margarodidae *sensu lato*, and at what level to classify taxa currently considered to be in these groups.

The latter is probably the major current controversy concerning the phylogeny and family-level classification of Coccoidea, and resolution is required for interpreting scale insect evolution. Taxa referred to informally as the archaeococcoids or archaeococcids (e.g., Miller, 1984; Gullan & Kosztarab, 1997; Cook *et al.*, 2002; Hodgson & Foldi, 2005, 2006) or the orthezioids or Orthezioidea (e.g., Koteja, 1974b; Danzig, 1980), comprise the Margarodidae *s. l.* (*i.e.*, *sensu* Morrison, 1927, 1928) (with over 400 species and now treated as at least 11 families; see below), Ortheziidae (ensign scales; about 190 species), Carayonemidae (4 species), Phenacoleachiidae (2 species), and sometimes also Putoidae (about 60 species) (Koteja, 1996; Foldi, 2001; Cook *et al.*, 2002; Gullan & Martin, 2003; Ben-Dov, 2005; Hodgson & Foldi, 2006). Collectively, the above archaeococcoid families only number approximately 100 genera and 700 species. All remaining scale insect species (over 7000) belong to 17 families (Ben-Dov *et al.*, 2006) that form a well-defined monophyletic group and are referred to informally as the "advanced" coccoid families, the neococcoids or neococcids (Gullan & Kosztarab, 1997; Cook *et al.*, 2002; Gullan & Martin, 2003) or Coccoidea *sensu stricto* (e.g. Koteja 1974b; Danzig 1980). In contrast, most morphological features that define the archaeococcoids are plesiomorphies that occur more widely in the Hemiptera (Schlee, 1969; Koteja, 1996) and, to date, morphological and molecular phylogenetic studies have failed to demonstrate monophyly of the archaeococcoids or the margarodids *s. l.* (Miller, 1984; Foldi, 1997; Cook *et al.*, 2002; Hodgson & Foldi, 2005).

Koteja (1974a,b) proposed a phylogeny and classification of the scale insects that gave family rank to a number of groups that were placed until recently within the Margarodidae *s. l.* Later he described or recognized several new extinct families (e.g. Koteja, 2000a, 2004; Koteja & Azar, in press) and presented fossil data to suggest that some archaeococcoids (at least margarodids *s. l.* plus ortheziids) represent the relics of an ancient radiation (e.g. Koteja, 1990, 1996, 2000a,b, 2001a). Representatives of a number of the archaeococcoid lineages are present in the fossil record earlier than almost all recognisable neococcoid lineages. Koteja (2001a,b) and Koteja & Azar (2001) recognized a diverse assemblage of archaeococcoid taxa plus at least one neococcoid taxon from the Early Cretaceous and suggested that extensive radiations of scale insects must have occurred during pre-Cretaceous times, despite the lack of definitive fossils. Koteja was ahead of his time in recognizing a number of families, such as Callipappidae, Coelostomidiidae, Kuwaniidae, Marchalinidae, Matsucoccidae, Monophlebidae, Pityococcidae, Steingeliidae, and Xylococcidae, for taxa that most of his contemporaries recognized as margarodid subfamilies or tribes, following the synthetic work of Morrison (1927, 1928). The morphological disparity of these various margarodid *s. l.* higher taxa (Morrison, 1928), their great age in the fossil record (e.g. Koteja, 2000a,b, 2001a, 2004) and also the difficulty of reconstructing their interrelationships using morphology of females and nymphs (e.g., Gullan & Sjaarda, 2001), suggest that Koteja's higher classification of the archaeococcoid taxa is justified. The recent systematic work of several authors has supported Koteja's classification (e.g. Foldi, 2004, 2005; Hodgson & Foldi, 2006; Miller *et al.*, 2007).

Few data are available currently with which to test the monophyly of the archaeococcoids. Relatively few phylogenetically informative morphological characters of females and nymphs can be scored across all coccoid taxa due to the combination of autapomorphic and plesiomorphic features exhibited by many groups. Morrison's traditional classification was based largely on the morphology of adult females, which is often highly derived and frequently involves reduction or loss of structures. Hodgson and Foldi (2005, 2006) have studied the morphology of macropterous adult males, for which character state homology is less problematic, but phylogenetic analyses to date have provided little support for relationships among most families (however some groupings are discussed below).

Given the apparent limitation of scale insect morphology for resolving scale insect higher phylogeny, it was anticipated that DNA sequence data would be useful in reconstructing scale insect relationships. The apparent antiquity of many lineages suggests that conserved gene regions are the most likely to resolve the deeper (*i.e.*, family-level) divergences within scale insects. The nuclear small subunit ribosomal RNA gene (SSU rRNA or 18S) has been used previously for addressing higher-level phylogenetic questions in Coc-

coidea (Cook *et al.*, 2002), but only seven archaeococcoid and 32 neococcoid taxa were included. The data were consistent with the monophyly of neococcoids but relationships among archaeococcoid taxa were unresolved. Our recent phylogenetic research using 18S and an expanded taxon set recovers a monophyletic neococcoid group (albeit with poor support) as well as the family-level groups recognized by Koteja, although the Iceryini is not grouped with the other Monophlebidae and most archaeococcoid family-group lineages stem from a basal polytomy (Fig. 1). The extent of 18S divergence among the coccoid families is as high as or higher than among the aphid families, consistent with Koteja's family-level classification for Coccoidea. Molecular data suggest that the ancestor of the extant families of Aphidoidea evolved in the late Jurassic or early Cretaceous, and that extant subfamilies and tribes radiated beginning in the late Cretaceous (von Dohlen & Moran, 2000; Havill *et al.*, 2007). It seems that the radiation of extant archaeococcoid families occurred well prior to that of extant aphid families. In addition, the lack of resolution recovered among scale insect families from 18S data and morphology indicates that the basal radiations might have been relatively rapid.

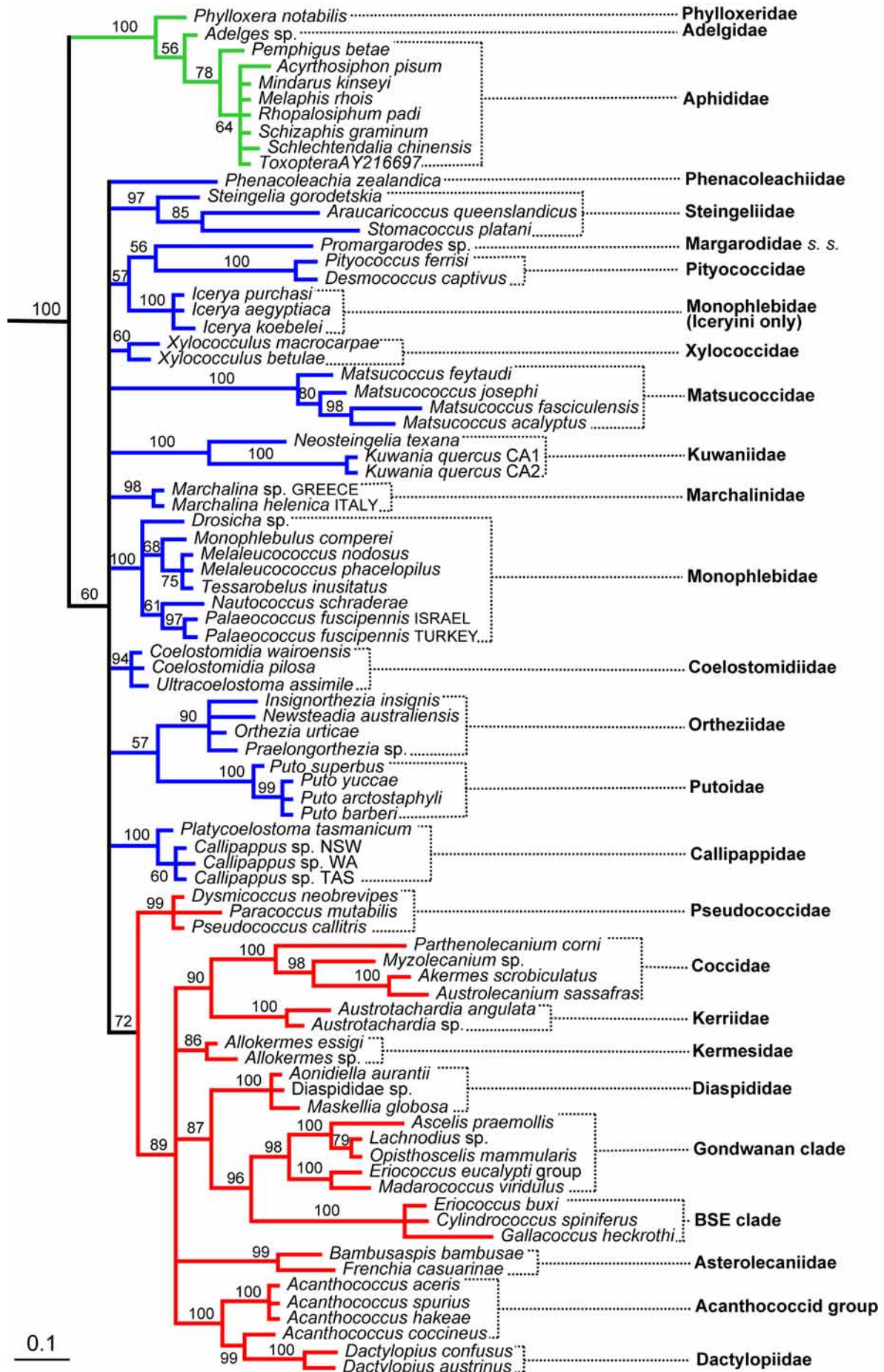
Below we review our current state of knowledge of the relationships and classification of the higher groups within scale insects, and suggest directions for future research. We arrange the discussion by the informal groupings of archaeococcoids and neococcoids.

A review of archaeococcoid classification and relationships

As summarised above, the extant archaeococcoids comprise the 11 families of the Margarodidae *sensu* Morrison (1927, 1928) plus the Ortheziidae, Carayonemidae, Phenacoleachiidae and Putoidae. In addition, 11 extinct families have been described, mostly based on adult males and including many amber inclusions (Koteja, 1989, 1990, 1998, 2000a,b, 2004; Koteja & Poinar, 2001; Koteja & Azar, in press).

The monophyly of each of the Carayonemidae, Ortheziidae and Phenacoleachiidae has never been questioned, although postulated relationships among these and the other archaeococcoid families are unresolved and often differ widely among studies based on different data sets (e.g., Miller, 1984; Cook *et al.*, 2002; Hodgson, 2002; Hodgson & Foldi, 2005). However, based on their morphology, it is possible that Carayonemidae is nested within the ensign scales, the Ortheziidae, with which it shares some putative synapomorphies (Kozár & Konczné Benedicty, 2000; Kozár & Foldi, 2002). The only phylogenetic analysis to include the Carayonemidae was based on morphological data (Foldi, 1997) and suggested that Carayonemidae was sister to a clade containing the Ortheziidae plus the neococcoids. Unfortunately, appropriately preserved carayonemids are unavailable for DNA sequencing because the group is extremely difficult to collect (Kozár & Foldi, 2002).

FIGURE 1. Phylogram from Bayesian analyses of nucleotide sequences (495 bp of unambiguous alignment from a total alignment of 780 bp) from the nuclear small subunit ribosomal RNA gene (SSU rRNA or 18S) obtained from 72 species of scale insects and rooted using 10 outgroup taxa from the three families of Aphidoidea (green). Neococcoid taxa are coloured red and groups considered archaeococcoids are in blue. Bayesian posterior probabilities (BPP) are listed above branches. Although some families are shown as sister taxa, BPP are typically low and therefore the relationships are not supported, with a few exceptions. In contrast, all families recognised here have BPP ($\geq 90\%$), except for Kermesidae and Xylococcidae. 37 species were newly sequenced for this study; data for 35 species were available from our previous work (Cook *et al.*, 2002) and sequences for the outgroups were obtained from GenBank [aphids: U27825, U27826, U27821, U27820, AY216697, U20411, U27819, U27824, U20400, U20398; scales: AY795507, U06475, AY795523, AY795521, AY795520, AY795530, AY795529, AY795513, AY795515, AY795512, AY795539, AY795540, AY795541, AY795536, U20402, AY795538].



Recently, the extant ortheziids were split into four subfamilies and nine tribes (Kozár 2004). Traditionally, the Ortheziidae has been grouped with the margarodids *s. l.* based on the shared possession of a few plesiomorphic features (such as the possession of abdominal spiracles), but ensign scales are separated as a distinct family because the adult females have stalked eyes, a distinctive sensillum at the apex of the distal antennal segment, and an anal ring with pores and setae that is more similar to the anal ring of neococcoids than that of other archaeococcoids (Williams & Watson, 1990; Miller *et al.*, 2005). A similar anal ring occurs in the Carayonemidae. Shcherbakov (2007) discussed putative plesiomorphies of ortheziids, and the lack of apomorphies for grouping ortheziids with either other archaeococcoids or with neococcoids. Some intuitive analyses (Miller & Kosztarab, 1979; Nur, 1980) have suggested that the Ortheziidae is sister to all other scales. Cladistic analyses of morphological data have generated conflicting results, albeit with little or no support. A study of adult males, using aphidoids as outgroups, placed the Ortheziidae as sister to all other scale insects except the Matsucoccidae (Hodgson & Foldi, 2005). Two cladistic studies based on morphological data from adult females, adult males and first-instar nymphs suggest that either ortheziids are sister to (*Pityococcus* McKenzie (*Phenacoleachia* Cockerell (*Puto* Signoret + neococcoids))) (Miller, 1984) or to *Phenacoleachia* + neococcoids (Foldi, 1997). Other morphological cladistic analyses (e.g., Gullan & Sjaarda, 2001; Hodgson, 2002) are uninformative on the relationships of the Ortheziidae because they have used this family as the outgroup. Maximum likelihood analysis of SSU rDNA based on a reduced taxon set put the single ortheziid as sister to the only included species of Putoidae (Cook *et al.*, 2002) and Bayesian analysis of an expanded taxon set recognised the same sister group relationship but without support (Fig. 1).

The Phenacoleachiidae is represented by one extant genus, *Phenacoleachia*, with two described species restricted to New Zealand and two subantarctic islands (Beardsley, 1964; Gullan and Cook, 2002; Miller *et al.*, 2005). On the basis of morphology, this family has been affiliated either with mealybugs (Pseudococcidae) (Cox, 1984; Miller and Miller, 1993), which are neococcoids, or placed with the archaeococcoids (Koteja, 1974a,b, 1996; Danzig, 1980). Analysis of SSU rDNA data placed *Phenacoleachia* in an unresolved position as part of a basal polytomy in Coccoidea (Cook *et al.*, 2002; also Fig. 1), whereas cladistic analysis of male morphological data suggested that Phenacoleachiidae is sister either to Putoidae alone (Hodgson, 2002) or to the group (*Puto* (*Steingelia* Nasonov (*Pityococcus* + Pseudococcidae)) (Hodgson & Foldi, 2005). Traditionally, *Steingelia* and *Pityococcus* are considered to be margarodids *s. l.* (e.g., Gullan & Sjaarda, 2001; Ben-Dov, 2005), except that *Pityococcus* was placed outside of the margarodids in one morphological cladistic analysis (Miller, 1984). The shared morphological features of Phenacoleachiidae, Pseudococcidae and Putoidae, such as dorsal ostioles, lateral clusters of wax-exuding structures (e.g., cerarii) and trilocular pores in the adult females may be symplesiomorphies (Danzig, 1980; Gullan & Cook, 2002). In the adult male, these groups (plus *Pityococcus* and *Steingelia*) are characterised by features such as loss of compound eyes, some eyes not placed laterally, the presence of a post-ocular ridge, forewings covered in microtrichia, and the presence in most taxa of glandular pouch setae on the posterior abdomen (Hodgson & Foldi, 2005).

The Putoidae contains only the genus *Puto*, which is distributed throughout the Holarctic and Neotropical regions (Ben-Dov *et al.*, 2006). Adult females are mealybug-like in appearance. *Puto* is putatively plesiomorphic in cytology (XX-XO) (Hughes-Schrader, 1944), and its endosymbionts are very different from those of mealybugs (Buchner, 1965; Tremblay, 1989). Traditionally, *Puto* was placed in the Pseudococcidae (Danzig, 1980; Kosztarab, 1996; Miller & Miller, 1993) based primarily on morphological similarities of the adult females, but molecular analysis suggests an ambiguous placement outside of the neococcoids (Cook *et al.*, 2002; also Fig. 1) and male morphology either puts it with *Phenacoleachia* in a clade sister to all neococcoids (Hodgson, 2002) or sister to a clade containing *Steingelia*, *Pityococcus* and mealybugs (Hodgson & Foldi, 2005). Whatever their relationships, Putoidae and Phenacoleachiidae must have diverged from the ancestor of neococcoids prior to the evolution of paternal genome elimination, which is a shared derived feature of neococcoids (Nur, 1980; Cook *et al.*, 2002; Normark, 2003). The earliest record of a fossil putoid is in Lebanese amber from the Early Cretaceous (Koteja, 2001a; Koteja & Azar, 2001, in press) but it is contemporaneous with the earliest known neococcoid (which Koteja assigned to a new family).

The group of 11 families treated formerly as Margarodidae *s. l.* was last reviewed comprehensively by Morrison (1928), who grouped the genera into five subfamilies (Table 1). Jakubski (1965) divided the ground-pearl group (hypogaecic margarodids), Margarodini *sensu* Morrison (1928), into two parts and elevated their rank to Margarodidae and Termitococcidae, but provided no alternative names or ranks for the other taxa of the margarodids *s.l.* Jakubski's higher-level nomenclature has been rejected or ignored by most subsequent workers. Koteja (1974a,b, 1996, 2000b, 2001a) considered most of Morrison's subfamilies or tribes to be families (Table 1), based primarily on detailed study of female mouthparts and adult male morphology. The findings of Hodgson & Foldi (2006) supported Koteja's classification and also justified the elevation the Stigmatococcini to family rank.

Many authors have considered whether the extant species of the Margarodidae *s. l.* constitute a monophyletic group, or are merely the paraphyletic remnant of Coccoidea after the other scale families are separately grouped (e.g., Boratynski & Davies, 1971; Miller & Kosztarab, 1979; Nur, 1980; Miller, 1984; Foldi, 1997; Gullan & Sjaarda 2001; Hodgson & Foldi, 2005), but there is no strong evidence either way. Hodgson & Foldi (2006) included nine family-level groups in their informal "margarodoids", which comprised the margarodids *s. l.* (i.e., *sensu* Morrison, 1927, 1928), excluding *Pityococcus* (Pityococcidae) and *Steingelia* plus *Stomacoccus* Ferris (Steingeliidae).

TABLE 1. Two divergent classifications of Margarodidae *sensu lato* based on extant taxa. (* Hodgson & Foldi (2006) placed these two families outside of margarodids *s. l.*; Gullan & Sjaarda (2001) transferred *Platycoelostoma* to tribe Callipappini.)

Classification of Morrison (1927, 1928) with addition of McKenzie (1942)	Classification of Koteja (1974a,b, 1990, 1996, 2000b) and Hodgson & Foldi (2006)
Subfamily Coelostomidiinae Tribe Coelostomidiini Tribe Marchalinini Tribe Pityococcini Tribe Platycoelostomini	Family Coelostomidiidae Family Marchalinidae Family Pityococcidae*
Subfamily Margarodinae Tribe Callipappini Tribe Kuwaniini Tribe Margarodini	Family Callipappidae Family Kuwaniidae Family Margarodidae [+ Family Termitococcidae in Koteja (1996)]
Subfamily Monophlebinae Tribe Drosichini Tribe Iceryini Tribe Llaveiini Tribe Monophlebini Tribe Monophlebulini	Family Monophlebidae
Subfamily Steingeliinae Tribe Steingeliini	Family Steingeliidae*
Subfamily Xylococcinae Tribe Matsucoccini Tribe Stigmatococcini Tribe Xylococcini	Family Matsucoccidae Family Stigmatococcidae Family Xylococcidae

A review of neococcoid classification and relationships

Neococcoids are characterised by features such as the loss of abdominal spiracles and the acquisition of paternal genome elimination (PGE) (Danzig, 1980; Nur, 1980; Cook *et al.*, 2002). In scale insect taxa with PGE, males start life as diploid zygotes but ultimately produce sperm that carry only their mother's genes, and thus are functionally haplodiploid (Normark 2003). Historically the neococcoids were divided into two informal groups—the diaspidoid and the lecanoid groups (see overview in Hodgson (1997)), on the basis of chromosome system. However, taxa with the diaspidoid system are nested among those with the lecanoid system, rendering the latter paraphyletic. The three largest families of neococcoids are the Diaspididae (ca 2,400 species of armoured scales), Pseudococcidae (ca 2,200 species of mealybugs) and Coccidae (ca 1,150 species of soft scales). The other neococcoid families are the Eriococcidae (ca 560 species of felt scales), the three pit scale families—Asterolecaniidae, Lecanodiaspididae and Cerococcidae—totalling about 350 species, Kerriidae (= Tachardiidae; ca 90 species of lac insects), Kermesidae (ca 90 species of gall-like scales), Acleridae (ca 60 species), and seven smaller families, listed in order of size—Conchaspidae, Halimococcidae, Stictococcidae, Beesoniidae, Dactylopiidae (cochineal insects), Micrococcidae and Phoenicococcidae—totalling about 100 species (Ben-Dov *et al.*, 2006). Future studies may show that some of these species-poor families are autapomorphic members of a larger group. For example, both Acleridae and Micrococcidae are similar to Coccidae (soft scales) (Hodgson, 1997; Miller & Williams, 1995) and, although used as outgroups to the Coccidae in the phylogenetic study of Miller & Hodgson (1997), their recognition at family rank may render the Coccidae paraphyletic. The Beesoniidae (beesoniids), Dactylopiidae (cochineal insects) and Stictococcidae (stictococcids) are each closely related to a subset of the Eriococcidae in molecular phylogenetic studies (Cook *et al.*, 2002; Cook & Gullan, 2004; Fig. 1). The Phoenicococcidae is monotypic and together with the Halimococcidae has affinities to the Diaspididae (Miller, 1990), with these three taxa often referred to as the diaspidoids, although their interrelationships are uncertain. The Conchaspidae shares some features with the diaspidoids and other features with more distantly related neococcoids, and its phylogenetic position is an enigma (see review in Ben-Dov (1990)).

Relationships among the 17 families of neococcoids are not well resolved at the basal nodes, although it seems that the mealybugs (Pseudococcidae) may be sister to all other groups (Miller, 1984; Cook *et al.*, 2002; Hodgson 2002; Fig. 1). The Coccidae is probably sister to the morphologically peculiar Kerriidae (Fig. 1), although morphology of adult males did not suggest this relationship (Hodgson, 2002). All recent phylogenetic studies with sufficient taxon sampling (Cook *et al.*, 2002; Cook & Gullan, 2004; Hodgson, 2002; Fig. 1) agree on the non-monophyly of eriococcids, as suggested earlier based on morphology (Cox & Williams, 1987). Phylogenetic analysis of 18S data (Cook & Gullan, 2004) recovered four groups within Eriococcidae: (i) the BSE clade, comprising representatives of the Beesoniidae and Stictococcidae and the eriococcid taxa *Cylindrococcus* Maskell, *Eriococcus buxi* (Boyer de Fonscolombe)—the type species of *Eriococcus* Targioni Tozzetti, and *E. williamsi* Danzig (Fig. 1 does not include *E. williamsi* or any stictococcid); (ii) a Gondwanan group comprising Australian and New Zealand taxa, many of which feed on Myrtaceae; (iii) the acanthococcid group comprising the type species of *Acanthococcus* Signoret if it is recognised as a genus separate from *Eriococcus*, plus other eriococcids from both the northern and southern hemispheres, and also *Dactylopius* Costa (family Dactylopiidae); and (iv) *Calycicoccus* Brain as an isolated lineage (Cook & Gullan, 2004; Gullan *et al.*, 2006) (this taxon is not included in Fig. 1). Postulated relationships among the diaspidoid families, the Diaspididae (armoured scales), Halimococcidae and Phoenicococcidae, and the tribes and subfamilies of the Diaspididae were reviewed by Miller (1990). The relationships of the diaspidoid group to the eriococcid groups and the pit scale families are uncertain (Fig. 1).

A few recent hypotheses of relationships for taxa within each of the three largest families of Coccoidea (Pseudococcidae, Diaspididae and Coccidae) are available, and several molecular and morphological phylogenetic studies are in progress. A higher classification of the Pseudococcidae into three subfamilies, Phen-

acoccinae, Pseudococcinae and Rhizoecinae, based on molecular data alone, was proposed by Downie & Gullan (2004). A revised classification based on an expanded taxon set and integrating molecular data with morphological data from adult males, adult females and first-instar nymphs found support for just two subfamilies, Phenacoccinae and Pseudococcinae (Hardy *et al.*, in press). The hypogaecic mealybugs were recognised as the tribe Rhizoecini within the Phenacoccinae, and there was support for the monophyly of the tribes Planococcini, Pseudococcini and Trabutinini within the Pseudococcinae. There have been various tribal and subfamilial classifications for the Diaspididae (see Ben-Dov, 1990; Miller, 1990; Takagi, 2002), but most agree on the major constituent tribes with the two largest being the Aspidiotini and the Diaspidini. Recent molecular phylogenetic analyses of the Diaspididae (Morse *et al.*, 2005; Morse & Normark, 2006) found reasonable agreement with the traditional morphology-based classification of Borchsenius (1965) and Takagi (2002). The current higher classification of the Coccidae was established by Hodgson (1994) who recognised 10 subfamilies (Coccinae with four tribes) and several unplaced genera, based on intuitive assessment of the morphology of adult females. A cladistic analysis of morphological characters of adult males and females and first-instar nymphs, using higher taxa as terminals, found support for the monophyly of Coccidae and for a group consisting of Ceroplastinae, Coccini, Pulvinariini and Saissetiini (Miller & Hodgson, 1997).

Future directions

There are many unresolved questions in scale insect phylogeny relating to relationships within and among families, and monophyly of major groups at family level and above. Answers to these questions will require both larger taxon sets and additional informative genetic markers. At present, the lack of resolution of relationships among archaeococcoid higher taxa using either morphological or molecular data (Fig. 1) is suggestive of a rapid radiation, but inclusion of additional genetic data might uncover a more hierarchical pattern of relationships. For example, current molecular phylogenies for the whole of Coccoidea are based only on a portion of the SSU rRNA gene, partly due to the inability to amplify some regions of the gene for all specimens and paralogy problems with other nuclear-encoded genes. Including the whole of 18S might enhance resolution. However, it may be impossible to resolve relationships among the families of the former Margarodidae *s. l.*, and among all archaeococcoid families, due to the likely great antiquity and persistence of the radiation. The same dilemma applies to many other groups of organisms, especially to taxa that diversified rapidly in the distant past (Whitfield & Lockhart, 2007).

Most species diversity of Coccoidea occurs within the neococcoid families Coccidae, Diaspididae and Pseudococcidae, and resolving the relationships of their constituent species and genera will provide more natural, and thus predictive, classifications of these economically important families. Within individual scale insect families, it seems likely that relationships will be resolved based on additional taxon sampling and diverse data sources, as exemplified by mealybugs (Hardy *et al.*, in press). One feasible additional data source is the DNA of scale insect primary endosymbionts. Phylogenetic relationships of these symbionts could be used to corroborate the phylogeny of their host scales, since these bacteria appear to co-speciate with their hosts (e.g., Downie & Gullan, 2005; Gruwell *et al.*, 2007). Progress is being made towards resolving internal relationships of the larger families of neococcoids using their DNA sequence data. More extensive taxon and gene sampling of armoured scales is underway with over 135 species and 80 genera so far (B.B. Normark, pers. comm.), and a molecular phylogenetic study based on at least 150 species of soft scales is in progress (T. Kondo & L.G. Cook, unpublished data). Despite the increasing numbers of molecular studies, morphological interpretations of hypotheses of relationships based on genetic data remain integral to the provision of any new intra-family classifications. Studies based on morphological data alone will provide independent phylogenetic hypotheses to be tested with molecular data, or tests of prior hypotheses developed from molecular data. For scale insects, morphological data from adult males is more likely to be informative on relationships

of higher taxa than morphological data from adult females, due to the wealth of male characters that can be homologised across even distantly related groups (Hodgson, 2002; Hodgson & Foldi, 2005, 2006). A phylogenetic study based on the morphology of adult male neococcoids is in progress (C.J. Hodgson, pers. comm.). The latter, together with the ongoing molecular studies, should culminate in a new family-level classification of all neococcoids in the near future.

Acknowledgements

Peter Cranston, Chris Hodgson, Takumasa Kondo and Zhi-Qiang Zhang provided helpful comments on a draft of the manuscript. This work was supported in part by a National Science Foundation PEET grant (DEB-0118718) to Penny Gullan, an Australian Research Council Discovery Project grant to Lyn Cook, and an Australian Biological Resources Survey grant to LGC and PJG.

References

- Beardsley, J.W. (1964) Insects of Campbell Island. Homoptera: Coccoidea. *Pacific Insects* (Monograph), 7, 238–252.
- Ben-Dov, Y. (1990) Classification of diaspidoid and related Coccoidea. In: Rosen, D. (Ed), *World Crop Pests, Volume 4A, Armored Scale Insects: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 97–128.
- Ben-Dov, Y. (2005) *A Systematic Catalogue of the Scale Insect Family Margarodidae (Hemiptera: Coccoidea) of the World*. Intercept Ltd, Wimborne, 400 pp.
- Ben-Dov, Y., Miller, D.R. & Gibson, G.A.H. (2006) ScaleNet. <http://www.sel.barc.usda.gov/scalenet/scalenet.htm> (Accessed 5 August and 10 September 2007)
- Blackman, R.L., & Eastop, V.F. (2000) *Aphids on the World's Crops. An Identification and Information Guide*. 2nd ed. John Wiley & Sons, Ltd, Chichester, 466 pp.
- Boratynski, K. & Davies, R.G. (1971) The taxonomic value of male Coccoidea (Homoptera) with an evaluation of some numerical techniques. *Biological Journal of the Linnaean Society*, 3, 57–102.
- Borchsenius, N.S. (1965) Bases of classification of armored scales. *Entomologicheskoe Obozrenie*, 44, 326–376.
- Bourgoin, T. & Campbell, B. (2002) Inferring a phylogeny for Hemiptera: falling into the 'autapomorphic trap'. *Denisia*, 4, 67–82.
- Buchner, P. (1965) *Endosymbiosis of Animals with Plant Microorganisms*. Wiley, New York, 909 pp.
- Cook, L.G. & Gullan, P.J. (2004) The gall-inducing habit has evolved multiple times among the eriococcid scale insects (Sternorrhyncha: Coccoidea: Eriococcidae). *Biological Journal of the Linnaean Society*, 83, 441–452.
- Cook, L.G., Gullan, P.J. & Trueman, H.E. (2002) A preliminary phylogeny of the scale insects (Hemiptera: Sternorrhyncha: Coccoidea) based on nuclear small-subunit ribosomal DNA. *Molecular Phylogenetics and Evolution*, 25, 43–52.
- Cook, L.G. & Rowell, D.M. (2007) Genetic diversity, host-specificity and unusual phylogeography of a cryptic, host-associated species complex of gall-inducing scale insects. *Ecological Entomology*, 32, 506–515.
- Cox, J.M. (1984) Relationships of the Phenacoleachiidae (Homoptera: Coccoidea). *Proceedings of the 10th International Symposium of Central European Entomofaunistics*, Budapest, 15–20 August 1983, 339–341.
- Cox, J.M. & Williams, D.J. (1987) Do the Eriococcidae form a monophyletic group? *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri'* 43 (Suppl.) (1986), 13–17.
- Danzig, E.M. (1980) *Coccoids of the Far East USSR (Homoptera, Coccinea) with Phylogenetic Analysis of Scale Insects Fauna of the World*. (In Russian). Nauka, Leningrad, Russia, 367 pp. [Also available in a 1986 English translation: Oxonian Press Pvt. Ltd, New Delhi, 450 pp.]
- Downie, D.A. & Gullan, P.J. (2004) Phylogenetic analysis of mealybugs (Hemiptera: Coccoidea: Pseudococcidae) based on DNA sequences from three nuclear genes, and a review of the higher classification. *Systematic Entomology*, 29, 238–259.
- Downie, D.A. & Gullan, P.J. (2005) Phylogenetic congruence of mealybugs and their primary endosymbionts. *Journal of Evolutionary Biology*, 18, 315–324.
- Foldi, I. (1997) Defense strategies in scale insects: phylogenetic inference and evolutionary scenarios (Hemiptera, Coccoidea). *Memoires du Museum National d'Histoire Naturelle (N.S.) Serie A, Zoologie*, 173, 203–230.
- Foldi, I. (2001) A world list of extant and fossil species of Margarodidae *sensu lato* (Hemiptera, Coccoidea). *Nouvelle Revue d'Entomologie*, 18, 195–231.

- Foldi, I. (2004) The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). *Annales de la Société Entomologique de France* (N.S.), 40, 145–168.
- Foldi, I. (2005) Ground pearls: a generic revision of the Margarodidae *sensu stricto* (Hemiptera: Sternorrhyncha: Coccoidea). *Annales de la Société Entomologique de France* (N.S.), 41, 81–125.
- Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, Cambridge, 755 pp.
- Gruwell, M.E., Morse, G.E. & Normark, B.B. (2007) Phylogenetic congruence of armoured scale insects (Hemiptera: Diaspididae) and their primary endosymbionts from the phylum Bacteroidetes. *Molecular Phylogenetics and Evolution*, 44, 267–280.
- Gruwell, M.E., von Dohlen, C.D., Patch, K. & Normark, B.B. (2005) Preliminary PCR survey of bacteria associated with scale insects (Hemiptera: Coccoidea). Proceedings of the X International Symposium of Scale Insect Studies, Adana, Turkey, 19th–23rd April 2004. pp. 101–116.
- Gullan, P.J. & Cook, L.G. (2002) *Phenacoleachia* Cockerell (Hemiptera: Coccoidea: Phenacoleachiidae) re-visited. *Bollettino di Zoologia agraria e di Bachicoltura*, Ser. II, 33, 163–173.
- Gullan, P.J., Downie, D.A. & Steffan, S.A. (2003) A new pest species of the mealybug genus *Ferrisia* Fullaway (Hemiptera: Pseudococcidae) from the USA. *Annals of the Entomological Society of America*, 96, 723–737.
- Gullan, P.J., Giliomee, J.H., Hodgson, C.J. & Cook, L.G. (2006) The systematics and biology of the South African gall-inducing scale insect *Calycicoccus merwei* Brain (Hemiptera: Coccoidea: Eriococcidae). *African Entomology*, 14, 13–33.
- Gullan, P.J. & Kosztarab, M. (1997) Adaptations in scale insects. *Annual Review of Entomology*, 42, 23–50.
- Gullan, P.J. & Martin, J.H. (2003) Sternorrhyncha (jumping plant-lice, whiteflies, aphids and scale insects). In: V. Resh & R. Cardé (Eds), *Encyclopedia of Insects*. Academic Press, pp. 1079–1089.
- Gullan, P.J. & Sjaarda, A.W. (2001) Trans-Tasman *Platycoelostoma* Morrison (Hemiptera: Coccoidea: Margarodidae) on endemic Cupressaceae, and the phylogenetic history of margarodids. *Systematic Entomology*, 26, 257–258.
- Hardy, N.B., Gullan, P.J. & Hodgson, C.J. (2008) A classification of mealybugs (Hemiptera: Pseudococcidae) based on integrated molecular and morphological data. *Systematic Entomology* (in press).
- Havill, N.P., Footitt, R.G. & von Dohlen, C.D. (2007) Evolution of host specialization in the Adelgidae (Insecta: Hemiptera) inferred from molecular phylogenetics. *Molecular Phylogenetics and Evolution*, 44, 357–370.
- Heie, O. (1999) Aphids of the past (Hemiptera, Sternorrhyncha). *Proceedings of the First Palaeoentomological Conference, Moscow, 1998, AMBA, Bratislava*, pp. 49–55.
- Hodgson, C.J. (1994) *The Scale Insect Family Coccidae: An Identification Manual to Genera*. CAB International, Wallingford, Oxon, UK, 639 pp.
- Hodgson, C.J. (1997) Classification of the Coccidae and related coccoid families. In: Ben-Dov, Y. & Hodgson, C.J. (Eds), *World Crop Pests, Volume 7A, Soft Scale Insects: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam & New York, pp. 157–201.
- Hodgson, C.J. (2002) Preliminary phylogeny of some non-margarodid Coccoidea (Hemiptera) based on adult male characters. *Bollettino di Zoologia agraria e di Bachicoltura*, Ser. II, 33, 129–137.
- Hodgson, C.J. & Foldi, I. (2005) Preliminary phylogenetic analysis of the Margarodidae *sensu* Morrison and related taxa (Hemiptera: Coccoidea) based on adult male morphology. *Proceedings of the X International Symposium of Scale Insect Studies, Adana, Turkey, April 2004*, pp. 35–47.
- Hodgson, C. & Foldi, I. (2006) A review of the Margarodidae *sensu* Morrison (Hemiptera: Coccoidea) and some related taxa based on the morphology of adult males. *Zootaxa*, 1263, 1–250.
- Hughes-Schrader, S. (1944) A primitive coccid chromosome cycle in *Puto* sp. *Biological Bulletin*, 87, 167–176.
- Jakubski, A.W. (1965) *A Critical Revision of the Families Margarodidae and Termitococcidae (Hemiptera, Coccoidea)*. British Museum (Natural History), London, 187 pp.
- Koteja, J. (1974a) Comparative studies on the labium in the Coccinea (Homoptera). *Zeszyty Naukowe Akademii Rolniczej w Krakowie, Rozprawy*, 89, 1–162.
- Koteja, J. (1974b) On the phylogeny and classification of the scale insects (Homoptera, Coccinea) (discussion based on the morphology of the mouthparts). *Acta Zoologica Cracoviensia*, 19, 267–326.
- Koteja, J. (1989) *Inka minuta* gen. et sp. n. (Homoptera, Coccinea) from Upper Cretaceous Taymyrian amber. *Annales Zoologici (Warsaw)* 43, 77–101.
- Koteja, J. (1990) Paleontology. In: Rosen, D. (Ed), *World Crop Pests, Volume 4A, Armored Scale Insects: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 149–163.
- Koteja, J. (1996) Scale insects (Homoptera: Coccinea) a day after. In: Schaefer, C.W. (Ed.), *Studies on Hemipteran Phylogeny*. Proceedings of Thomas Say Publications in Entomology, Entomological Society of America, Lanham, Maryland, pp. 65–88.
- Koteja, J. (1998) Essays on coccids (Homoptera): sudden death in amber? *Polskie Pismo Entomologiczne* 67, 185–218.
- Koteja, J. (2000a) Scale insects (Homoptera, Coccinea) from Upper Cretaceous New Jersey amber. In: Grimaldi, D. (Ed.), *Studies on Fossils in Amber, with Particular Reference to the Cretaceous New Jersey*. Backhuys, Leiden, The Netherlands, pp. 147–229.

- Koteja, J. (2000b) Advances in the study of fossil coccids (Hemiptera: Coccinea). *Polskie Pismo Entomologiczne*, 69, 187–218.
- Koteja, J. (2001a) Essays on coccids (Hemiptera: Coccinea): paleontology without fossils? *Prace Muzeum Ziemi*, 46, 41–53.
- Koteja, J. (2001b) Pre-Cretaceous scale insects (Hemiptera: Coccinea). In: Krzeminska, E. & Krzeminski, W. (Eds), *Abstracts Volume. Second International Congress on Palaeontology. Fossil Insects*. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, pp. 31–32.
- Koteja, J. (2004) Scale insects (Hemiptera: Coccinea) from Cretaceous Myanmar (Burmese) amber. *Journal of Systematic Palaeontology*, 2, 109–114.
- Koteja, J. & Azar, D. (2001) Lower Cretaceous scale insects (Hemiptera: Coccinea) from the Hammana outcrops in central Lebanon. In: Krzeminska, E. & Krzeminski, W. (Eds), *Abstracts Volume. Second International Congress on Palaeontology. Fossil Insects*. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, pp. 30–31.
- Koteja, J. & Azar, D. (2008) Scale insects from Lower Cretaceous amber of Lebanon (Hemiptera: Sternorrhyncha: Coccinea). *Alavesia*, 2 (in press).
- Koteja, J. & Poinar, O. (2001) A new family, genus and species of scale insect (Hemiptera: Coccinea: Kukaspididae, new family) from Cretaceous Alaskan amber. *Proceedings of the Entomological Society of Washington*, 103, 356–363.
- Kozár, F. (2004) *Ortheziidae of the World*. Plant Protection Institute, Hungarian Academy of Sciences, Budapest, Hungary, 525 pp.
- Kozár, F. & Foldi, I. (2002) The water scale insects of the mysterious family Carayonemidae (Hemiptera: Coccoidea). *Bollettino di Zoologia Agraria e di Bachicoltura* (Milano), Ser. II, 33(2001), 197–201.
- Kozár, F. & Konczné Benedicty, S. (2000) Carayonemidae of the Neotropical region with the descriptions of new genera and species (Homoptera: Coccoidea). *Folia Entomologica Hungarica*, 61, 71–82.
- Kosztarab, M. (1996) *Scale Insects of Northeastern North America: Identification, Biology, and Distribution*. Virginia Museum of Natural History, Martinsville. Special Publication No. 3, 650 pp.
- Miller (1984) Phylogeny and classification of the Margarodidae and related groups (Homoptera: Coccoidea). *Proceedings of the 10th International Symposium of Central European Entomofaunistics*, Budapest, 15–20 August 1983: pp. 321–324.
- Miller, D.R. (1990) Phylogeny. In: Rosen, D. (Ed), *World Crop Pests, Volume 4A, Armored Scale Insects: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 169–178.
- Miller, D.R. & Davidson, J.A. (1990) A list of the armored scale insect pests. In: Rosen, D. (Ed), *World Crop Pests, Volume 4B, Armored Scale Insects: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 299–306.
- Miller, D.R., Gimpel, M.E. & Rung, A. (2005) *A Systematic Catalogue of the Cerococcidae, Halimococcidae, Kermesidae, Micrococcidae, Ortheziidae, Phenacoleachiidae, Phoenicococcidae and Stictococcidae (Hemiptera: Coccoidea) of the World*. Intercept Limited, Wimborne.
- Miller, D.R. & Hodgson, C.J. (1997) Phylogeny. In: Ben-Dov, Y. & Hodgson, C.J. (Eds), *World Crop Pests, Volume 7A, Soft Scale Insects: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam & New York, pp. 229–250.
- Miller, D.R. & Kosztarab, M. (1979) Recent advances in the study of scale insects. *Annual Review of Entomology*, 24, 1–27.
- Miller, D.R. & Miller, G.L. (1993) A new species of *Puto* and a preliminary analysis of the phylogenetic position of the *Puto* group within the Coccoidea (Homoptera: Pseudococcidae). *Jeffersoniana: Contributions from the Virginia Museum of Natural History* (4), 1–35.
- Miller, D.R., Rung, A., Venable, G.L. & Gill, R.J. (2007) Scale insects: identification tools for species of quarantine importance. Scale Families. ARS & APHIS, USDA. Available from: <http://www.sel.barc.usda.gov/ScaleKeys/ScaleInsectsHome/ScaleInsectsFamilies.html> (accessed 5 September 2007).
- Miller, D.R. & Williams, D.J. (1995) Systematic revision of the Family Micrococcidae (Homoptera: Coccoidea), with a discussion of its relationships, and a description of a gynandromorph. *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri'*. *Portici* 50 (1993), 199–247.
- Morrison, H. (1927) Descriptions of the genera and species belonging to the coccid family Margarodidae. *Proceedings of the Biological Society of Washington*, 40, 99–109.
- Morrison, H. (1928) A classification of the higher groups and genera of the coccid family Margarodidae. *United States Department of Agriculture Technical Bulletin*, 52, 1–239.
- Morse, G.E., Gruwell, M.E., Claps, L.E. & Normark, B.B. (2005) Towards a combined molecular and morphological phylogenetic analysis of the Diaspididae. In: Erkili, L.B. & Kaydan, M.B. (Eds), *Proceedings of the X International Symposium of Scale Insect Studies, ISSIS-X*, 19–23 April, 2004, Adana, Turkey, pp. 79–99.
- Morse, G.E. & Normark, B.B. (2006) A molecular phylogenetic study of armoured scale insects (Hemiptera: Diaspididae). *Systematic Entomology* 31, 338–349.
- Normark, B.B. (2003) The evolution of alternative genetic systems in insects. *Annual Review of Entomology*, 48, 397–423.

- Nur, U. (1980) Evolution of unusual chromosome systems in scale insects (Coccoidea: Homoptera). In: R.L. Blackman, G.M. Hewitt, & M. Ashburner (Eds.), *Insect Cytogenetics*. Royal Entomological Society, London, pp. 97–117.
- Nur, U., Brown, S.W. & Beardsley, J.W. (1987) Evolution of chromosome number in mealybugs (Pseudococcidae: Homoptera). *Genetica*, 74, 53–60.
- Remaudière, G. & Remaudière, M. (1997) *Catalogue of the World's Aphididae. Homoptera: Aphidoidea*. Institut National de la Recherche Agronomique, Paris. 473 pp.
- Robison, W.G. (1977) Ultrastructure of Coccoidea sperm. *Bulletin of the Virginia Polytechnic Institute and State University Research Division* 127, 35–50.
- Robison, W.G. (1990) Sperm ultrastructure, behaviour, and evolution. In: Rosen, D. (Ed), *World Crop Pests, Volume 4A, Armored Scale Insects: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 205–220.
- Schaefer, C.W. (Ed.) (1996) *Studies on Hemipteran Phylogeny*. Proceedings of Thomas Say Publications in Entomology, Entomological Society of America, Lanham, Maryland. 244 pp.
- Schlee, D. (1969) Die Verwandtschaftsbeziehungen innerhalb der Sternorrhyncha aufgrund synapomorpher Merkmale. *Stuttgarter Beiträge zur Naturkunde*, 199, 1–19.
- Shcherbakov, D.E. (2007) Extinct four-winged precoccids and the ancestry of scale insects and aphids (Hemiptera). *Russian Entomological Journal*, 16, 47–62.
- Shcherbakov D.E. & Wegierek P. (1991) Creaphididae, a new and the oldest aphid family from the Triassic of Middle Asia. *Psyche*, 98, 81–85.
- Sorensen, J.T., Campbell, B.C., Gill, R.J. & Steffen-Campbell, J.D. (1995) Non-monophyly of Auchenorrhyncha ("Homoptera"), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-Heteropteroidea Hemiptera (s.l.) and a proposal for new monophyletic suborders. *Pan-Pacific Entomologist*, 71, 31–60.
- Takagi, S. (2002) One new subfamily and two new tribes of the Diaspididae (Homoptera: Coccoidea). *Insecta Matsumurana* 59(N.S.), 55–100.
- Takagi, S. (2007) The gall-inducing coccoid family Beesoniidae (Hemiptera): facts, speculations, and perspectives. *Oriental Insects*, 41, 67–91.
- Tremblay, E. (1989) Coccoidea endocytobiosis. In: Schwemmler, W. and Gassner, G. (Eds) *Insect Endocytobiosis: Morphology, Physiology, Genetics, Evolution*. CRC Press, Boca Raton, FL, pp. 145–173.
- von Dohlen, C.D. & Moran, N.A. (1995) Molecular phylogeny of the Homoptera: a paraphyletic taxon. *Journal of Molecular Evolution*, 41, 211–223.
- von Dohlen, C.D. & Moran, N.A. (2000) Molecular data support a rapid radiation of aphids in the Cretaceous and multiple origins of host alternation. *Biological Journal of the Linnean Society*, 71, 689–717.
- Whitfield, J.B. & Lockhart, P.J. (2007) Deciphering ancient rapid radiations. *Trends in Ecology and Evolution*, 22, 258–265.
- Williams, D.J. & Watson, G.W. (1990) *The Scale Insects of the Tropical South Pacific Region. Part 3. The Soft Scales (Coccidae) and Other Families*. CAB International Institute of Entomology, Wallingford, Oxon, UK, 267 pp.

