A TIME SCALE FOR SCALES: RECONCILING NEONTOLOGY AND PALEONTOLOGY IN Coccoidea (Hemiptera)

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A TIME SCALE FOR SCALES: RECONCILING NEONTOLOGY AND PALEONTOLOGY IN COCCOIDEA (HEMIPTERA)

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ABSTRACT

Scale insects (Hemiptera: Coccoidea), with 8,000 species, 33 Recent and 19 extinct families, are amongst the most destructive insects in agriculture. Perhaps 98% of the species feed on angiosperms. The superfamily is traditionally divided into the primitive archaeococcoids and the derived neococcoids, the latter with 90% of the species. The neococcoids were hypothesized to have diversified in response to the radiation of angiosperms ca. 100 Ma. Despite a sophisticated taxonomy based almost exclusively on the conspicuous neotenic adult females, there is a paucity of higher-level phylogenetic studies, and this compromises evolutionary understanding. Fossil scale insects are diverse in ambers around the world, 135 to 20 Ma, but are preserved mostly as the highly dissimilar winged adult males, adding a challenge in understanding the relationships of fossil taxa. My dissertation is aimed at reconciling paleontology and neontology in Coccoidea and testing whether the neococcoids diversified as a result of the angiosperm radiations.

My approach was to first assess whether fossil scale insects could be incorporated in a phylogenetic framework. To begin, I used the Ortheziidae (ensign scale insects), a morphologically well-defined family, where morphological features and fossil evidence suggests an early origin of the family in Coccoidea evolution. Based on 69 morphological
characters of female ortheziids and using 39 exemplar Recent species, I provide the first 
analytical assessment of relationships among Recent and extinct genera of the family. 
Fossils included eight species, based on complete, well-preserved specimens in amber 
from 125-20 Ma (unlike other coccoid groups, ortheziids are fossilized mostly as 
females). Five new species and one new genus of fossil ensign scales are described from 
three amber deposits.

Second, it was necessary to understand macropterous male morphology. 
However, because adult male Coccoidea do not feed and rarely live more than three or 
four days, they are seldom collected and their morphology has been little studied. In the 
Ortheziidae, for example, males of only four extant and three fossil species were known, 
in a family of over 200 species. Herein, the detailed male morphology of seven 
previously described species is provided, which, by knowing males of three additional 
genera, provides significantly better understanding of male morphological variation in 
Ortheziidae. The utility of laser confocal microscopy for the study of old, rare, uncleared 
collection slide preparations is shown to allow better visibility of macrostructures, but not 
for minute structures such as pores.

A comprehensive study was made of macropterous males in four amber deposits: 
Eocene of the Baltic region and India (Cambay amber), mid-Cretaceous of Myanmar, and 
Early Cretaceous of Lebanon. Descriptions of 16 new species, 11 new genera, and three 
new families are provided, including very important records for six Recent families, such 
as the first fossil Margarodidae (Cambay amber) and another definitive Cretaceous 
neococoid (in Burmese amber). These fossils are then discussed in a phylogenetic
framework, obtained from analyzing 123 Recent and fossil taxa for 169 morphological characters.

Finally, I assess whether fossil information can help resolve deep-node relationships in Coccoidea. Estimates of divergence times of the major lineages are made based on morphological and molecular data, and lineage ages are discussed with major biotic events in earth history. This study presents the first total-evidence (vs. node-calibrated) approach to phylogenetic assessment for the Coccoidea, using 169 morphological characters and regions of the 18S, 28S and EF-1a genes. The taxon sampling includes 73 Recent and 43 fossil terminals covering 48 of the 54 recognized families in Coccoidea. Despite the large proportion of missing data and a very heterogeneous dataset, results indicate that most of the Recent families of Coccoidea were established by 100 Ma, revealing that the divergence of neococcoid families may have not affected by the angiosperm radiations. The origin of Coccoidea is estimated as Late Triassic, ca. 220 Ma.
To my father, Van Vea
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CHAPTER I

INTRODUCTION

The seminal and highly cited paper by Ehrlich and Raven (1964) developed the theory that phytophagy has great effects on the radiations of insects, an idea very much alive today (Janz, 2011). Given that insects are the premier predators of land plants, with nearly half of all described insect species feeding directly on plant tissue (Grimaldi & Engel, 2005), the evolutionary role of plants in the diversification of insects is a question of profound consequences, not just conceptually but also practically (e.g., pest management). The traditional consensus is that the diversification of angiosperms provided myriad new adaptive niches, and thus accelerated the rate of speciation of the insects feeding on them. Several studies, however, independently report that some groups of insects radiated well after the divergences of their angiosperm hosts (e.g., McKenna et al., 2009; Percy et al., 2004), which has fundamental implications for studies of co-speciation and co-phylogeny. Are such lags the norm between phytophagous insects and their angiosperm hosts? One hemipteran group Coccoidea can provide an exemplary model for testing this hypothesis.

With nearly 8,000 described species, the superfamily Coccoidea is a major monophyletic group of phytophages. The adult females are sedentary and suck plant sap with mouthparts modified into stylets. Associated with their immobility are specializations such as reduction to complete loss of appendages and the development of protective secretions (Gullan & Kosztarab, 1997), the latter to counter predators and desiccation. Scale insects are usually found in large populations on a host plant as parasites, decreasing the fitness of their host. Because several species are polyphagous,
especially in the most diverse families (i.e. Coccidae, Pseudococcidae and Diaspididae), they have significant impacts in agriculture and horticulture, occasioning billions of dollars in damage annually (Kosztarab, 1990). This damage is generally not directly created by the scale insect itself, but by opportunistic organisms such as fungi, developing on the plant after being weakened by the slow removal of vascular fluids (Perrin & Malphettes, 1974) or by transmission of virus and other diseases by the plant feeder (Hogenhout et al., 2008).

In addition to their bizarre morphologies, scale insects have evolved diverse, unique, genetic sex-determination systems. The most widespread such system is the paternal genome elimination (PGE), a haplodiploid mechanism in which males are first diploid zygotes, to ultimately produce gametes only carrying their maternal genome (Normark, 2003). These genetic systems are related to different reproductive strategies, which range from regular sexual reproduction to independent evolution of parthenogenesis and in some rare cases hermaphroditism (in the genus Icerya) (Gullan & Kosztarab, 1997). Scale insects also possess a diversity of maternally-transmitted bacterial endosymbionts (Büchner, 1965; Gruwell et al. 2005; 2007; 2010), which apparently played a significant role in the evolution of coccoids. Ross et al. (2012) showed that some endosymbionts are responsible for the transition between diplodiploidy to male haploidy, leading inter alia to PGE.

As Sternorrhyncha, which commonly produce honeydew from plant fluids, scale insects have also developed biotic interactions with ants, ranging from simple honeydew harvesting by the ants (this is widespread among many coccoid families), to trophobiosis and an exchange of honeydew for protection by ants against predators and parasites.
(Hölldobler & Wilson, 1990; Delabie, 2001). Highly specialized, obligate mutualisms occur in some tribes of Pseudococcidae (Schneider & LaPolla, 2011), which has existed between certain mealybugs and *Acropyga* ants for at least 20 millions years (Johnson et al., 2001).

Scale insects, with aphids (Aphidoidea), whiteflies (Aleyrodoidea) and jumping plant lice (Psylloidea) form the suborder Sternorrhyncha. Sternorrhynchans are characterized by the position of the mouthparts on the sternal region. This feature is probably an adaptation resulted from an exclusively phytophagous lifestyle with relative immobility, as opposed to other Hemiptera (Grimaldi & Engel, 2005). The sister group of Coccoidea is consensually agreed to be the Aphidoidea (von Dohlen & Moran, 1995; Sorenson et al., 1995; Bourgoin & Campbell, 2002).

The superfamily includes more than 7,900 species classified into 33 Recent families (Ben-Dov et al., 2013). Coccoids have exceptional morphological diversity of basic body plans and specialized features, particularly in comparison to their sister group Aphidoidea (4,400 species in 10 families: Remaudière & Remaudière, 1997) and which is partly reflected by many more higher-level groups in Coccoidea. As mentioned previously, one hallmark feature of coccoids is their extreme sexual dimorphism, with females having a truncated life cycle and maturing into a paedomorphic, wingless stage with eyes, antennae, and legs highly reduced to lost. Alternatively, the males have a very different life cycle, undergoing a quiescent pupal stage referred to as neometaboly (Bellès, 2011); the mature male emerges devoid of functional mouthparts but otherwise completely developed and winged. The morphological differences are so dramatic that association of males and females of the same species is impossible other than by direct
observation of copulating pairs, or rearing them from immatures on the same host plant (COI sequencing will be helpful, but is not yet applied for this purpose). In addition, most coccoid systematics is based on the paedomorphic females, resulting in virtual ignorance of adult males by comparison. Foundational studies have produced for male morphology of the major neococcoid families (Afifi, 1968; Ghauri, 1962; Giliomee, 1967) as well as a few representatives of archaeococcoids (Theron, 1958), but much detailed and extensive study of the archaeococcoid families has only recently increased for several families (e.g. Hodgson & Foldi, 2006; Hodgson et al., 2007). Male morphology has been shown to be informative for taxonomic ranking and classification. For instance, the Margarodidae sensu Morrison (1928) comprised subfamilies and tribes that are now defined as families. This classification was recently adopted (e.g., Hodgson & Foldi, 2006), although first hypothesized by Koteja (1974, 1996, 1998, 2000) on the basis of morphological mouthparts of the females, adult males and fossils. Most recently, the taxonomic utility of adult males has been verified by the recognition of a new Recent family, the Rhizoecidae based on adult males (Hodgson, 2012).

Scale insects are informally divided into two main groups: (i) the “primitive” grade of archaeococcoids (Bodenheimer, 1952; Borscheinius, 1958), which currently includes the Recent Ortheziidae, Putoidae, Phenacoleachiidae, Marchalinidae, Matsucoccidae, Monophlebidae, Coelostomidiidae, Margarodidae, Xylococcidae, Kuwaniidae, Steingeliidae, Pityococcidae, Stigmacoccidae and Callipappidae. Collectively, species of archaeococcoids comprise only 9% of the Recent Coccoidea and have been defined by plesiomorphic characters, such as the presence in males of compound eyes and abdominal spiracles. The other grouping is a monophyletic lineage,
the neococcoids, and includes the other 7,300 species of scale insects, defined by the absence of abdominal spiracles and compound eyes in adult males and the presence of paternal genome elimination (Gullan & Cook 2007; Cook et al., 2002). The neococcoids include 18 Recent families, the largest being the mealybugs (Pseudococcidae), soft scale insects (Coccidae) and armored scale insects (Diaspididae).

Fossil Coccoidea have been the subject of comprehensive taxonomic work, but almost exclusively by the late Jan Koteja. Koteja was a talented and fastidious morphologist who dedicated the last 20 years of his research to the description and characterization of coccoids in amber. He described more than 30 species and 16 families based on fossilized adult males in majority, in ambers from deposits covering more than 100 million years. From his deep understanding of Recent and fossil taxa, and coccoid morphology, Jan Koteja provided intuitive hypotheses of relationships between extinct and extant families (Koteja, 2001; summarized in Grimaldi & Engel, 2005).

Phylogenetic studies of Coccoidea are fairly recent, the main reason being that adult female morphology is so reduced and convergent that homology assessments are limited and challenging. Phylogenetic hypotheses were, however, developed using a limited number of molecular markers and morphological characters for a few specific families: Pseudococcidae (Downie & Gullan 2004; Hardy et al., 2008), Eriococcidae (Cook & Gullan, 2004), and Diaspididae (Andersen et al., 2010; Morse & Normark, 2005). As for phylogenetic relationships among families, there have been a few studies with limited taxon sampling using ribosomal (Cook et al., 2002) or mitochondrial markers (Yokogawa & Yahara, 2009), and a larger taxon representation with one ribosomal sequence (Gullan & Cook, 2007) and adult male morphology (Hodgson &
Foldi, 2005; Hodgson & Hardy, 2013). In these studies, the neococcoids are monophyletic and the archaeococcoids are paraphyletic, as expected. Additional relationships among archaeococcoid families are unclear or not well supported, although Hodgson & Hardy (2013) provide a strong foundation from the morphological perspective. A clarification of the relationships among these families would allow a better understanding of the early evolution of Coccoidea.

Two main hypotheses have been postulated with regard to scale insect origin and evolution. Borchsenius (1958) hypothesized that most of the families were established before the Cretaceous and that the original host plants were gymnosperms, especially conifers. The alternative hypothesis favors a recent diversification of scale insects, being a consequence of the flowering plant radiation and giving rise to the speciose neococcoid families (Hoy, 1962; Danzig, 1980).

In the context of these two hypotheses, this dissertation addresses the following questions:

- What are the phylogenetic relationships amongst fossil and Recent taxa? Do Cretaceous taxa, for example, represent stem groups to living families? By necessity this requires morphology, which provides an opportunity to also compare estimates of divergence time based on the phylogeny of Recent and fossil taxa with molecular estimates.
- Was scale insect evolution driven by the diversification of flowering plants? One approach to this question is assessing chronology, specifically testing whether the Coccoidea radiation (particularly the diverse, modern groups of
angiosperm-feeders) coincided with that of angiosperms. Did it precede or lag behind that of angiosperms?

- Besides angiosperms, another major group with which coccoid symbiose is ants. Does the first fossil appearance and/or radiation of major lineages of ant-tended coccoids (e.g., pseudococcids) coincide with the early lineages of ants in the Cretaceous, or with the major radiation of dolichoderine, myrmecine, and formicine ants in the Paleocene and Eocene? These are the groups today the largely tend pseudococcids.

The dissertation chapters, presented here, address the diversity and relationships of extinct and Recent Coccoidea, including their interpretation in a phylogenetic framework.

The Ortheziidae has traditionally been considered one of the most basal families of Coccoidea (Koteja, 1986), currently comprising 200 described species classified into 22 genera (Kozár, 2004). Several comprehensive taxonomic works on the family had been published over the last 90 years (see Vea & Grimaldi [2012] for review), but phylogenetic hypotheses among subfamilies and major genera were lacking. Additionally, for only five of the 200 species have had their adult males described in detail (Koteja, 1986; Hodgson & Foldi, 2006). Unlike other coccoid families, most fossil ortheziids are females, probably because adult females of the family are more mobile and thus more likely to encounter resin flows. Ortheziidae was an attractive subject for a dissertation chapter because the family was considered ancient; it was monographed and the species-level taxonomy well established (Kozár, 2004), with a manageable number of taxa; and there existed adult female inclusions in amber from ca. 125 to 20 Ma, some even with
their ovisacs containing first-instar nymphs. Chapter II is the first phylogenetic study of the family Ortheziidae, and the first such study in Coccoidea that includes fossil and extant taxa.

In order to incorporate fossils into phylogenetic studies, knowledge and expertise in male morphology is essential. Chapter III describes the adult males for seven species of the Ortheziidae classified into five different genera; previously, males were known for only five species and two genera. This chapter adds to a growing body of knowledge on male coccoids, namely on the neococcoids (Afifi, 1968; Ghauri, 1962; Giliomee, 1967), and Margarodidae sensu lato (Hodgson & Foldi, 2006; Hodgson et al., 2007; Koteja, 1986; Theron, 1958).

Building upon the tradition in the study of fossil coccoids established by Koteja, diverse new coccoids in four major amber deposits have been recovered, prepared, studied and described. The majority of taxa described here is Cretaceous and could not be placed within the current concepts of known families. Chapter IV describes 16 new species, 11 new genera and three new families in Early and mid-Cretaceous amber from Lebanon and Myanmar, respectively, and in Eocene amber from India and the Baltic region. All descriptions are discussed in a phylogenetic framework, inferred upon 169 morphological characters and compared with almost all Recent recognized families.

Finally, Chapter V presents the first divergence time estimation of scale insect lineages, using the morphological characters from Chapter IV, molecular data (18S, 28S and EF-1a), and including 75 Recent and 43 fossil taxa in 48 families. For this study a method was used that was modified from MrBayes 3.2.1 (Ronquist et al., 2012), allowing the treatment of fossil taxa as terminals for inferring node dates. With the relationships of
fossil and Recent taxa, comparisons of coccoid diversification are made to that of their primary hosts – angiosperms – and their primary insect symbionts, ants.
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CHAPTER II

PHYLOGENY OF ENSIGN SCALE INSECTS (HEMIPTERA: COCCOIDEA: ORTHEZIIDEAE)
BASED ON THE MORPHOLOGY OF RECENT AND FOSSIL FEMALES


Abstract

The Ortheziidae (ensign scale insects) is a morphologically well-defined family. The morphology and occurrence in the fossil record suggests a probable early origin of the family in scale insect evolution. The present phylogenetic analysis – based on 69 morphological characters of female ortheziids, using 39 exemplar Recent species – provides the first analytical assessment of relationships among living genera of the family, as well as the relationships of eight fossil species, based on complete, well-preserved specimens in amber. Monophyly of the subfamilies Newsteadiinae, Ortheziinae and Ortheziolinae is supported, but Nipponortheziinae is found to be paraphyletic by inclusion of the Ortheziolinae. Thus, the subfamily Ortheziolinae is reduced in rank to tribe Ortheziolini stat.n., which now includes Matileortheziola Kozár & Foldi, Ortheziolacoccus Kozár, Ortheziolamameti Kozár and Ortheziola Šulc. Consequently, the tribes Matileortheziolini, Ortheziolacoccini and Ortheziolamametini are synonymized (syn.n.) here under Ortheziolini. Five new species and one new genus of fossil ensign scales are described from three amber deposits: Burmorthezia gen.n. with type species Burmorthezia kotejai sp.n. and also B. insolita sp.n., both in mid-Cretaceous Burmese amber (98 Ma) and Arctorthezia baltica sp.n. in Eocene Baltic amber (ca. 43 Ma) based
on second-instar nymphs; *Mixorthezia kozari* **sp.n.** and *M. dominicana** **sp.n.** in Miocene Dominican amber (ca. 17 Ma) based on adult females. Fossil placements are unambiguous, with *Burmorthezia* forming a stem to crown-group (Recent and Tertiary) Ortheziidae. A summary of described fossil ortheziids is provided.

**Introduction**

Taxonomic research on the Coccoidea, a group of approximately 8000 species (Ben-Dov *et al.*, 2011), has greatly advanced as a result of the needs of applied entomology. At present, the most inclusive group of Coccoidea is the monophyletic but informal neococcoid group (including the mealybugs and 16 other families), and the much less diverse, paraphyletic grade of approximately 15 families of archaeococcoids (Gullan & Cook, 2007). Most taxonomic research has focused on the neococcoids, which are highly significant in agriculture and comprise approximately 90% of the world species of Coccoidea. However, understanding the evolution of Coccoidea in general requires a more rigorous understanding of the archaeococcoids, including their fossils. As expected, fossils of coccoids are rarely preserved in sedimentary rocks because (with a few exceptions) the females are sedentary or sessile on their host plants. The winged males are ephemeral and details of their generally minute bodies are difficult to resolve in rock of all but the finest grains. The earliest definitive fossil coccoids are a few wings in shale from the early Cretaceous of England and Siberia, which bear series of fine, pinnate grooves distinctive to the Recent family Matsucoccidae (Koteja, 1988, 1999). A putative, undescribed coccoid from the late Jurassic exists (Grimaldi & Engel, 2005), but otherwise the Jurassic existence of Coccoidea can be inferred based on: (i) the diversity of archaeococcoids in seven families (six extant) from the Early Cretaceous (summarized
in Grimaldi & Engel, 2005), indicating that some divergence must have been Jurassic; and (ii) the sister-group relationship of the Coccoidea and Aphidoidea (Börner, 1904; Schlee, 1969; Grimaldi, 2003), the latter of which has several stem-group species from the Late Triassic and crown-group species from the Jurassic (Shcherbakov & Wegierek, 1991; Heie, 1996; Grimaldi & Engel, 2005). For unexplained reasons, in the Early Cretaceous (Valanginian and later, ca. 130 Ma), various conifers began producing large amounts of resin, which continues to the present day (Grimaldi & Engel, 2005). The resin entrapped insects and other small organisms prior to fossilizing as amber, and this has left an exceptionally rich fossil record. Also, because of preservation with microscopic fidelity, fossils in amber afford unique opportunity for phylogenetic study of extinct taxa. Coccoids, particularly the adult males, are among the most abundant insect group in the 25 or so major deposits of fossiliferous amber, all of which gives the scale insects one of the best fossil records in Insecta for the past 130 Ma (Grimaldi & Engel, 2005).

Fortunately, the study of coccoids in amber has a firm foundation, owing almost entirely to the work of the late Jan Koteja (Koteja, 1984, 1990, 1996, 2000a, b, 2001, 2004; Koteja & Azar, 2008). Koteja was an excellent morphologist and taxonomist (Wegierek, 2005; Dziedzicka & Podsiadlo, 2008; Gullan, 2008), who devoted the last two decades of his career to detailed descriptions of species of fossil coccoids, and he had an excellent intuitive understanding of relationships between Recent and fossil taxa (summarized in Grimaldi & Engel (2005): fig. 8.31, table 8.4). However, the fossils, indeed the morphology of Recent archaeococcoids, have rarely been studied in a phylogenetic context (Gullan & Sjaarda, 2001; Hodgson & Foldi, 2005). This seriously compromises not only interpretation of such a rich fossil record, but also an understanding of coccoid
evolution, about which there are some significant questions. A natural starting point for studying the phylogeny and fossil record of coccoids involves the Ortheziidae. This family is considered as morphologically well defined by features unique to the group, but its relationships with the rest of the Coccoidea remains unclear. The Ortheziidae have a combination of character states that are both plesiomorphic (e.g. the presence of abdominal spiracles) and apomorphic (e.g. the presence of an anal ring bearing pores and setae), in comparison with the neococcoids. More than two decades of study has not clarified the position of the family (details summarized in Gullan & Cook, 2007).

The Ortheziidae

Historically, the Ortheziidae, or ensign scale insects, have been considered to be one of the most ancient families of the Coccoidea (Koteja, 1986), being either an ‘ancestor’ to all scale insects (Borchsenius, 1958) or a ‘primitive’, isolated branch of the grade of families, the archaeococcoids (Koteja, 1974b; Danzig, 1980). Females are distinctive, possessing well-developed legs and antennae, and having much of the body cloaked in bundles of extravagant, white wax secretions, giving them a peculiarly ornate appearance (Fig. 2.1E). There are about 200 described species of Ortheziidae to date (Miller et al., 2011), classified within 22 genera (including four extinct genera) (Kozár, 2004). Only a few species of ortheziids are serious pests, such as the greenhouse ensign scale (Insignorthezia insignis [Browne]). The phytophagous species of ortheziids feed on the roots and/or stems of about 100 plant families (Miller et al., 2011), predominantly in the Asteraceae (asters) and Poaceae (grasses), and such ensign scales can occur in dense infestations. Although very little is known of the diet of the majority of Ortheziidae, these
Figure 2.1. Exemplar female specimens of Recent Ortheziidae species. A–D. Slide-mounted specimens, ventral view (wax lobes removed), A. *Newsteadia floccosa* (De Geer), B. *Nipponorthezia obscura* Morrison, C. *Orthezia cacticola* Morrison, D. *Orthezia newcomers* Morrison, E. *Orthezia graminicola* Morrison, unmounted specimen showing natural arrangement of wax lobes. Not to the same scale.
occur sporadically in leaf litter (presumably feeding on roots and fungal mycelia), and some are assumed to feed on mosses and lichens, habits that are putatively the most primitive in Coccoidea (Koteja, 1986; Kozár, 2004). The most recently described species of Ortheziidae, *Acropygorthezia williamsi* LaPolla et al. (2008), is the only ensign scale known to be an inquiline of ants; in this case with the subterranean species *Acropyga myops* Forel. *Acropyga* ants are well known for their obligate symbiosis with pseudococcids, an association that extends to at least the Miocene (Grimaldi & Engel, 2005; Johnson et al., 2001).

*Ortheziid taxonomy*

The first comprehensive taxonomic study of the Ortheziidae was by Morrison, who treated the group originally as a subfamily of the Coccidae (Morrison, 1925) and subsequently as a family (Morrison, 1952). His revision provided detailed illustrations of adult females, including comparisons among species of such structures as the eye, body spines and the anal ring. Photographs of ortheziids in natural habitus were provided, which is significant because scale insects are studied traditionally by slide mounting, which dissolves waxy exudations, and the structure and arrangement of the wax lobes is informative when differentiating ortheziid genera. For instance, Newsteadia Green can generally be easily recognized by median wax lobes inclined anteriad, instead of all lobes inclined posteriad in all other Ortheziidae (Kozár, 2004). Major taxonomic works subsequent to Morrison were published on *Newsteadia* (Kozár & Konczné Benedicty, 1999, 2000, 2001; Miller & Kozár, 2002) and *Ortheziola Šule* (Kozár & Miller, 2000). These workers were followed by an authoritative, worldwide, taxonomic revision of the family, in which four subfamilies were recognized (Kozár, 2004). Today, the family is
considered to comprise four subfamilies with nine tribes, 18 living genera and four extinct genera. The classification of the Ortheziidae provided by Kozár (2004) is given in Table 2.1 fossil taxa are summarized in the taxonomic section, below. Males of Ortheziidae are very rare and few have been described, namely: Newsteadia floccosa (De Geer), Orthezia urticae (Linnaeus) and Orthezia sp. by Koteja (1986), and Hodgson & Foldi (2006) illustrated and described a species of Orthezia from Colombia. Newsteadia floccosa is found frequently in leaf litter and O. urticae is a common pest of various perennial plants, sometimes occurring in high-density infestations (Kozár, 2004). Because most male specimens are collected in leaf litter traps, usually they cannot be associated with females. However adult males of a significant number of species reside in the major coccoid collections, remaining undescribed.

Fossils

Ortheziid fossils are rare. Koteja (2000a) recorded 22 specimens in Baltic amber, or approximately 2% of all Coccoidea in that amber. Six species of fossil ortheziids have been described to date (below), all except one of which derive from Baltic amber, the world’s largest and best studied deposit of amber (e.g., Weitschat & Wichard, 1998). Ochyrocoris electrina Menge was the first fossil ortheziid to be described, but according to Koteja (1988) the original specimen was lost; based on the simple description, he assumed it was a species of Arctorthezia Morrison. The Baltic amber fossils include two species in two extant genera (Arctorthezia antiqua Koteja & Zak-Ogaza and Newsteadia succini Koteja & Zak-Ogaza), and four extinct genera, Cretorthezia Koteja & Azar, Palaeonewsteadia Koteja, Protorthezia Koteja and Ochyrocoris Menge. The former three are based on adult male specimens only. Cretorthezia hammanaica Koteja & Azar, in
Table 2.1. Classification of the Recent Ortheziidae after Kozár (2004), with distributions and major host plant groups and habitats.
<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Tribe</th>
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<th># species</th>
<th>Geographic distribution of genus</th>
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<td>Poaceae and Compositae</td>
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<td>Pinaceae and Cactaceae</td>
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<td>Ortheziola</td>
<td>Ortheziola Šul</td>
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<td>Acropygorthzia La Polla &amp;</td>
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<td>Australia</td>
<td>Underground, plant root</td>
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</tbody>
</table>
Early Cretaceous amber from Lebanon, is the only species not preserved in Baltic amber, although Koteja & Azar (2008) indicated that assignment to the Ortheziidae was not definitive.

**Phylogenetic studies**

The only phylogenetic analysis for species within the Ortheziidae concerns *Ortheziola* (Kozár & Miller, 2000). This study mentioned a preliminary family-level phylogenetic analysis that proposed *Nipponorthezinella guadalcanalia* (Morrison) as the sister group to *Ortheziola*. This hypothesis was presented in the monograph by Kozár (2004), which included mainly genera of the Ortheziolinae. No molecular phylogeny of the family has been published. Only three species (*Nipponorthezia ardisiae* Kuwana, *Orthezia yashushii* Kuwana and *Orthezia* sp.) have COI-COII sequences available in GenBank (Benson *et al.*, 2011). Two previous molecular phylogenies of the scale insects have used 18S sequences of *Insignorthezia insignis*, *Newsteadia australiensis* Kozár & Konczné Benedicty, *Orthezia urticae* and *Praelongorthezia* sp. (Cook *et al.*, 2002; Gullan & Cook, 2007), but the sequences are not publicly available.

Here we present a phylogenetic analysis of the Ortheziidae based on female morphological characters and incorporate fossil taxa. This study, the first such analysis of scale insects in which fossil taxa are included, (i) assesses the relationships among genera of the family, (ii) tests the classification of Kozár (2004), and (iii) estimates the chronology and approximate divergence times of major lineages. Five species represented by adult females for two species and second-instar nymphs for three species, preserved with microscopic detail in amber from the Tertiary and Cretaceous, are
described. These are highly significant new fossil records and are crucial to estimation of
divergence times.

Materials and methods

Amber

Three amber deposits with ortheziid specimens were studied. The oldest deposit is
from the mid-Cretaceous of northern Myanmar, which is the largest and most diverse
deposit of Cretaceous amber. Burmese amber has been dated biostratigraphically from
late Albian to Cenomanian (c. 105 to 95 Ma), based respectively on an ammonite and
palynology (Cruickshank & Ko, 2003), and the insects preserved within it (Grimaldi et
al., 2002). Most recently, Burmese amber has been dated radiometrically at 98.8 °± 0.6
Ma using 206Pb/238U in volcanically-derived zircons (Shi et al., 2012). The zircons
were extracted directly from matrix surrounding nodules of amber. This age places the
origin of Burmese amber almost exactly at the Albian–Cenomanian boundary
(Obradovich, 1993; Gradstein et al., 2004). The age of Baltic amber inclusions are known
with less precision, because the material is acquired commercially, and the main deposits
at Yantarnyi, Samland Peninsula (near Kaliningrad) Russia, vary in age from early
Eocene (Ypresian), ca. 49–52 Ma, to late Eocene (Bartonian, ca. 37–38 Ma). The great
concentration of Baltic amber, however, comes from the Blau Erde stratum, which is
Lutetian (40–45 Ma) (Ritzkowskii, 1997), so an approximation of 43 Ma is reasonable for
the age of the inclusions studied here. Dominican amber is Miocene in age, ca. 15–18 Ma
and derives from mines in the Cordillero Septentrional in northern Dominican Republic,
approximately 10–20 km north and northeast of Santiago (Grimaldi, 1995; Iturralde-Vinent & MacPhee, 1996). Despite a span of 80 Ma among the three deposits, all seem to
have been formed in humid to wet forests that were subtropical or fully tropical. Burmese amber was derived from a conifer, the family of which is contentious [Pinaceae, Araucariaceae and Cupressaceae have been proposed (reviewed in Shi et al. (2012))].

The Baltic amber forest was dominated by pines, but with some oaks and other angiosperm trees, and Dominican amber was formed by *Hymenaea* (Fabaceae) trees in a lowland tropical paleoenvironment very similar to that found today in Central America and the Caribbean. The adult males of various Coccoidea can be abundant in various ambers around the world, but females are extremely rare, and female Ortheziidae in particular have been found in only the three amber deposits studied here, plus the Lebanese amber. Amongst approximately 3000 arthropod inclusions in Burmese amber (Grimaldi et al., 2002), just five ortheziid specimens (four juveniles and one adult male) were found (0.001%), and this proportion is even smaller for Dominican amber.

All amber pieces are in the Division of Invertebrate Zoology, American Museum of Natural History, where they were prepared by trimming and polishing according to the protocol in Nascimbene & Silverstein (2000), such that flat surfaces close to the inclusions maximized full dorsal and ventral views. Some specimens were embedded in a high quality epoxy under vacuum prior to trimming and polishing (Nascimbene & Silverstein, 2000), particularly those with fractures lying close to the inclusion. Ortheziid inclusions were studied and photographed by applying one of the flat surfaces to a microscope slide with a drop of glycerine, and applying a coverslip to the upper, flat surface close to the inclusion using another drop of glycerine. Microscopic study used stereomicroscopes (20°— to 140°—) and a Wild compound microscope (100–400x), using transmitted and reflected fiber-optic lights. Photomicrographs were made using an
Infinity(R) long-distance magnifying lens, MicrOptics(R) fiber optic flashes, and a Nikon D1X camera.

**Terminology and identification of life stage in amber**

The family has distinct wax secretions compared to the rest of the Coccoidea, which make them easy to recognize, but different wording has been used to define these secretions. We use terms used for the wax secretion as follows: wax lobes refer to the actual white secretions (‘tufts’ in Morrison (1925, 1952)), usually appearing as lobe-shaped (Fig. 2.1E); wax plates are as introduced by Kozár & Miller (2000), each being a ‘cluster of spines and pores that are distributed on the integument’ (Kozár & Miller, 2000: 16), visible when the adult female is slide-mounted (Fig. 2.1A–D) and from which the wax lobes are secreted. Wax plates correspond to the ‘derm spines arranged in clusters’ in Morrison (1925). Although Kozár & Miller (2000) created a system to define the homology of individual wax plates across Ortheziola, this system is not used here to code characters although we have defined a main area of wax plates to count them.

According to Sikes (1928), *Orthezia urticae* has four life stages for the females, the fourth stage being the adult. Assignment of a specimen with certainty to the adult stage is the presence of an ovisac, or in the case of slide-mounted specimens, the presence of an ovisac band. In the case of fossils in amber, specimens with an ovisac are identified easily to the adult stage. When the ovisac is absent, usually the third-instar nymph is similar to the young adult. To identify the life stage of fossil specimens, we considered the size of the individual and relative sizes of the appendages to the body, the extent of
wax secretion, the number of antennal segments, the position of the anal ring and the number of wax lobes.

*Phylogenetics*

In order to develop a hypothesis of relationships for the Ortheziidae, we coded all the adult female of the type species for each genus in the family [with the exception of *Ochyrocoris* sp., *Palaeonewsteadia huaniae* Koteja, *Protorthezia aurea* Koteja, *Cretorthezia* spp. and *Orthezinella hispanica* (Silvestri)], for a total of 17 genera. Additional species were added for the following genera: *Arctorthezia* (2 spp.), *Graminorthezia* Kozár (2), *Mixorthezia* Morrison (1), *Newsteadia* (6), *Nipponorthezia* Kuwana (1), *Orthezia* Bosc d’Antic (4) and *Praelongorthezia* Kozár (1), to better represent the current diversity in each genus. Some species were included because associated male specimens were available, housed in the collection of the U.S. National Museum of Natural History (USNM) (most of them remaining undescribed). Eight fossil species are represented in this analysis, with five new species described here [*Burmorthezia kotejai* sp.n., *B. insolita* sp.n. from Burmese amber, *Arctorthezia antiqua*, *A. baltica* sp.n. and *Newsteadia succini*, from Baltic amber, *Mixorthezia kozari* sp.n., *M. dominicana* sp.n. and *Nipponorthezinella* sp. from Dominican amber]. As *Burmorthezia* and *Arctorthezia baltica* are only represented by probably second-instar nymphs, some characters occurring on adults were not coded. For fossil taxa, this only included the number of antennal segments. *Icerya purchasi* Maskell (Monophlebidae), *Matsucoccus gallicolus* Morrison (Matsucoccidae), *Pseudococcus longispinus* (Targioni Tozzetti) (Pseudococcidae) and *Puto yuccae* (Coquillet) (Putoidae) were selected as outgroups. Extant taxa were coded according to observations of slide-mounted specimens from the
USNM, using a WILD M20-50998 compound microscope. Literature on the Ortheziidae was used for coding some taxa. A total of 69 morphological characters of the adult female were coded, for which details and illustrations are presented in ‘Results’ below. Forty-seven characters are binary and 22 are multistate. We decided to leave multistate characters as non-additive. Although some characters could have been coded as additive, we find no evidence for any of those characters to support such coding. For instance, the number of antennal segments, if treated as additive, would probably favor a tendency for antennal segment reduction, but we prefer not to impose such a priori constraint on the analysis. Morphological data were assembled into a matrix (Appendix A Table S2.1), available also in Morphobank (O’Leary & Kaufman, 2007) as project P610. Analyses were performed using TNT (Goloboff et al., 2008). The run was conducted using the following commands after holding 10 000 trees in memory: mult = tbr replic 10 000 hold 100. Bootstrap values (Felsenstein, 1985) were calculated for the resulting strict consensus tree: resample boot replic 10000. Because Acropygorthezia obviously displays many reductions in female features, an analysis was performed to test the effects of inclusion/exclusion of A. williamsi on relationships and support values (Appendix A Figure S2.1).
Results and discussion

Taxonomy

Family Ortheziidae

*Burmorthezia* Vea & Grimaldi gen.n.

*Type species: Burmorthezia kotejai* Vea & Grimaldi sp.n., by present designation.

*Description based on second-instar nymph.* Body elongate oval, dorsoventrally flattened. Antennae 6-segmented, inserted ventrally at frontal margin; with filiform segments and apical segment slightly clavate. Second segment bears stiff, erect, spine-like setae on lateral surface, other segments have numerous, undifferentiated setose setae. Eyes not easily observable, inserted on short stalks. Labium apparently 2-segmented. Legs well-developed, more slender than usual for ortheziids; trochanter distinctly separated from femur; tibia with about 15 rows of setae, all setose, tarsus with numerous similar setae, tibia and tarsus well separated; tibia without digitules; claw small, slightly bent, with hair-like digitules and without denticle. Anal ring visible on dorsum, relatively large, from which several setae and wax secretions protrude. Spiracles, body pores and most body setae not visible except for marginal setae. Wax secretion of ortheziid type, with nine marginal lobes, one frontal lobe, and at least 11 unseparated, segmentally divided median lobes (head region not visible). All wax lobes protrude posterioriad. Ovisac absent.

*Diagnosis.* Although only second-instar nymphs are known for *Burmorthezia* gen.n., they differ from other Ortheziidae known nymphs by the presence of fully transverse wax lobes (vs. laterally divided), apical segment without apical seta (vs. differentiated apical seta, blunt or hair like), second segment with two longer stiff setae (vs. none), trochanter
fully separated from femur (vs. trochanter fused to femur). Koteja & Azar (2008) described a specimen, tentatively identified as an ortheziid, in Early Cretaceous Lebanese amber, ‘?Cretorthezia sp.’ (unnamed), which bears similar features regarded as plesiomorphic. They pointed out that this specimen might be an older nymph or a young adult female, but could neither identify the stage with any certainty, nor ascertain whether it was associated with the adult male of Cretorthezia. Although the latter specimen has the same number of antennal segments (6) as Burmorthezia, the marginal wax lobes are completely different in having many more, thinner wax lobes (18 vs. 9 for Burmorthezia), as well as a flower-like arrangement that is not found in Burmorthezia. Koteja & Azar (2008) described Cretorthezia and assigned it to the Ortheziidae based on an adult male specimen from the same deposit as the putative female ‘?Cretorthezia sp. larva’, but expressed their doubts as to the placement of the female based on the plesiomorphic features. Burmorthezia has wax lobes typical of the Ortheziidae, but has features that are strikingly plesiomorphic compared with those of Tertiary and Recent Ortheziidae. These features include the absence of differentiated apical setae on the antennae; long, slender antennal segments; long, slender tibiae and tarsi; and a fully separated trochanter and femur. The anal ring is present on the dorsum but is visibly larger than that of the Recent Ortheziidae. The ring bears probably more than six setae (as in the Recent Ortheziidae) although the exact number is not visible. The wax secretion protruding from the anal ring partly obscures the ring, but this kind of secretion is specific to the Ortheziidae.

Etymology. The prefix of the genus name refers to Burmese amber, in which the specimens were discovered; the suffix of the name is common for genera in the Ortheziidae.
Comment. Burmorthezia was described as a new genus based on the observation of seven different specimens. Although antennal segmentation suggests that it is an immature (probably second-instar nymph considering the wax ornamentation and the size of the individuals), the specimens are undoubtedly a new morphogroup that has never been observed in scale insects, and thus requires documentation and description.

*Burmorthezia kotejai* Vea & Grimaldi sp.n.

(Figures 2.2A, C; 2.3)


*Description.* Second-instar nymph. Body elongate oval, 1.6 mm long, 0.95 mm wide, dorsoventrally flattened. Antennae 6-segmented, inserted ventrally at V-shaped frontal margin, distance between antennae 145 µm; with apical segment slightly clavate. Average antennal segments lengths in µm: First segment 125, Second segment 230, third segment 235, fourth segment 200, fifth segment 130, apical segment 210; antenna approximately 1.13 mm long. Second segment bears two stiff, erect, spine-like setae on lateral surface (about 65 µm), flagellar segments with numerous, undifferentiated setae, approx. 38 µm in length). Eyes not easily observable, inserted on short stalks. Mouthparts
Figure 2.2. Photomicrographs of *Burmorthezia* Vea & Grimaldi gen.n. in 98 million-year-old Burmese amber, all dorsal views. A. *B. kotejai* Vea & Grimaldi sp.n., holotype, B. *B. insolita* Vea & Grimaldi sp.n. holotype, C. *Burmorthezia* sp. (undetermined to species based on preservation).
Figure 2.3. Drawings of *Burmorthezia kotejai* Vea & Grimaldi gen.n., sp.n. (holotype) in Burmese amber. A. Detail of prothoracic leg, B. Detail of distal portion of antenna, C. Dorsal habitus, D. Ventral habitus, devoid of wax lobes. A, B to same scale; C, D to same scale.
with visible labium apparently 2-segmented. Legs well-developed, more slender than for usual ortheziids, long; coxa c. 100 µm long, trochanter distinctively separated from femur, both 500 µm; tibia 535 µm, with about 20 rows of setae, all setose, about 50 µm long; tarsus 260 µm with numerous similar setae, tibia and tarsus well separated; without digitules; claw small, 56 µm, slightly bent, with hair-like digitules and without denticle.

Anal ring visible on dorsum as a rounded structure, from which a few setae (number not determined) and wax secretions protrude. Spiracles, body pores and most body setae not visible except for marginal setae, with one long seta (80 µm) on each abdominal segment. Wax secretion of ortheziid type, with apparently nine marginal lobes, one frontal lobe, and at least 11 unseparated, transverse median lobes (head region not visible). All wax lobes protrude posteriad. Adult female and male unknown.

**Diagnosis.** Distinguished from *Burmorthezia insolita* sp.n. by the narrower and longer first segment relative to other antennal segments, V-shaped (vs. flat) frontal margin, and setae on legs about twice the length of those in *B. insolita*.

**Etymology.** In tribute to the late Jan Koteja, who has contributed significantly to the study of fossil scale insects.

**Burmorthezia insolita** Vea & Grimaldi sp.n.  
(Figures 2.2B, 2.4)


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Figure 2.4. Drawings of Burmorthezia insolita Vea & Grimaldi gen.n., sp.n. (holotype) in Burmese amber. A. Detail of distal portion of antenna, B. Entire antenna, also showing position of eye, C. Mesothoracic leg, D. Dorsal habitus, as preserved. B, C to same scale.
Description. Second-instar nymph. Body elongate oval in shape, 1.8 mm long with wax secretion, 0.85 mm wide, dorsoventrally flattened, although the specimen is ventrally retracted, resulting in a concave specimen. Eye on short stalk, with single facet/ommatidium. Antennae 6-segmented; inserted ventrally on flat frontal margin, distance between antennae 148 µm, apical segment slightly clavate; approximate antennal length 1.1 mm. Segmental lengths in µm: first segment 135, second segment 260, third segment 160, fourth segment 180, fifth segment 148, apical segment 225. Second segment bears two stiff, erect, spine-like setae (about 80 µm), segments 3–6 have numerous undifferentiated setose setae, c. 45 µm long. Eyes protruding but seem to be partially enveloped by cuticular structure. Mouthparts not clearly visible. Legs well developed, very slender; coxa not clearly visible, about 120 µm long, trochanter distinctively separated from femur, both 500 µm; tibia 700 µm, with 15–20 rows of setae, all setose, about 25 µm long; protarsus 180 µm, meso- and metatarsi about 260 µm each, with numerous similar setae, tibia and tarsus completely separated; without digitules; claw small and thin, about 55 µm long, with a pair of hair-like digitules and without denticle. Anal ring can be located on venter as a rounded structure with a few short setae. Spiracles, body pores and most body setae not visible except for numerous long marginal setae (lengths 100–150 µm) arranged as a row on each abdominal segment. Wax secretion of ortheziid-type, marginal lobes are most visible ones, with several having detached. Left side in dorsal view has one short subfrontal lobe and five attached marginal lobes, right side has one subfrontal lobe and six marginal lobes. Wax lobe present posteriorly. Median wax lobes seem to have been detached except for several
small ones remaining on dorsum. All wax lobes protruding posteriorad.

Adult female and male unknown.

*Diagnosis.* See diagnosis of *Burmorthezia kotejai* sp.n. Although *B. insolita* sp.n. bears wax secretions of an ortheziid type, the antennal and leg features (no differentiated apical seta, more slender and long setose setae) differ from the other Recent and Tertiary Ortheziidae.

*Etymology.* The species epithet comes from the Latin ‘insolita’ which means unusual referring to the morphological features of this fossil ortheziid.

*Arctorthezia Cockerell, 1902*

*Diagnosis.* Adult female: antennae 7-/8-segmented, apical seta short and spine-like, legs with tarsus and tibia well separated, nine pairs of dorsal marginal wax plates, with three triangular midline plates (in fossils, rectangular wax lobes). Current *Arctorthezia* spp. have a Nearctic and Palearctic distribution.

*Arctorthezia baltica* Vea & Grimaldi sp.n.

(Figures 2.5C, 2.6)

*Types.* Holotype. One complete second-instar nymph, amber piece number Ba-JVe38, Ex: Jurgen Velten collection (2010), housed at the American Museum of Natural History. Type locality and horizon. Baltic Region, presumably Lutetian-aged Blau Erde horizon of Yantarnyi, western Russia.

*Description.* Second-instar nymph. Body broadly oval in shape (best seen ventrally), 2.1 mm long, 1.68 mm wide (exclusive of wax lobes), dorsoventrally flattened. Antennae 6-segmented, inserted at frontal margin ventrally, slightly V-shaped, distance between antennae 228 µm, 6-segmented, with apical segment parallel-sided; approximate antennal
Figure 2.5. Photomicrographs of *Arctorthezia* spp. in Eocene (c. 43 Ma) Baltic amber. A, B. *Arctorthezia* sp. This species differs from *A. baltica* (shown in Fig.2.5C) by shapes of wax lobes and larger body size, but cannot be described because of obscured details, C. *Arctorthezia baltica* Vea & Grimaldi *sp.n.* holotype, dorsal view. To same scale.
Figure 2.6. Drawings of *Arctorthezia baltica* Vea & Grimaldi sp.n. in Baltic amber.  
A. Ventral habitus, as preserved (the entire venter has a short coat of wax, exclusive of appendages), B. Detail of entire left antenna, ventral view, C. Detail of labium, in slightly oblique posteroventral view, D. Detail of left mesothoracic leg, ventral view. B, C to same scale.
length 1.08 mm. Segmental lengths in \(\mu m\): first segment 173, second segment 185, third segment 198, fourth segment 142, fifth segment 136, apical segment 247. Setae sparse on all antennal segments, with one or two setae on first and second, followed by short, spine-like setae on segments 3 to 6. Last three segments with short, flagellate setae. Apex of apical segment with a short, stout, differentiated apical seta. Eye stalked, with one ommatidium. Mouthparts with labium visible, short with narrow apex, apparently 2-segmented, with numerous fine setulae. Legs well developed, rather slender; coxa c. 155 \(\mu m\) long, trochanter fused with femur, together 625 \(\mu m\); tibia 485 \(\mu m\), with 4–5 rows of setae, all spine-like; tarsus 375 \(\mu m\), with numerous similar setae, without digitules; claw 43 \(\mu m\) long, without denticles or large, spike-like claw digitules. Wax covering of Arctorthezia-type. Thick marginal lobes in ten pairs; frontal lobes triangular, well separated and extensively protruding from body margin, separated from lateral lobes. Lateral marginal lobes subrectangular, almost of same size from anterior to posterior. Caudal wax lobes separated from lateral ones. Dorsal wax lobes with nine submedian pairs, three asymmetrical median lobes, shield-like and of equivalent size from the second to fourth submedian lobes. Spiracles, body circular pore clusters separate marginal and submedian lobes anteriorly. Short coat of wax filaments entirely covering ventral surface (Fig. 2.6A: dotted lines). Ovisac absent. Adult female and male unknown.

**Diagnosis.** Arctorthezia baltica **sp.n.** is similar to *A. pseudoccidentalis* Morrison in the presence of nine circular pore clusters separating marginal and dorsal wax plates (vs absent in other species). The presence of multiple ommatidia (Koteja & Zak-Ogaza, 1988a) in Arctorthezia antiqua could not be confirmed after observation of the holotype specimen (adult female) in the Natural History Museum, London (Cocc-113), because it
was completely covered in organic particles. Additionally, observation of this holotype revealed eight pairs of marginal, one pair of frontal, one pair of posterior wax lobes; median wax lobes present, longer and triangular in shape; although covered by bubbles, no circular pore clusters between marginal and submedian lobes were observed, confirming that *A. antiqua* is different from *A. baltica* sp.n. Another specimen of *Arctorthezia* was found (cf. Fig. 2.5A, B) but given the state of the amber piece, it was impossible to obtain enough information to confirm that it belongs to *A. baltica* sp.n. Given the general shape of the median wax lobes and dimension of the posterior lobes, we think it ought to be described as a new species when more observation is obtained, such as from microtomography.

**Etymology.** The terminology refers to the vast Baltic amber deposit in which the species was discovered.

**Comment.** In *Arctorthezia*, the first- and second-instar nymphs have six antennal segments and the third-instar nymph has seven antennal segments (D.R. Miller, personal communication). Although the number of wax plates tends to increase as they mature, the specimen we described has adult-like wax secretion: Ten marginal wax lobes (including front and posterior lobes), nine dorsal clearly separated dorsal lobes and the triplet of midline lobes. On the basis of antennal segmentation, we have assigned the specimen described to a second-instar nymph. However, it was described here because the presence of clusters of circular pores allows a differentiation from *Arctorthezia antiqua*.

**Mixorthezia Morrison, 1925**

**Diagnosis.** Adult female: Four-segmented antennae, apical seta long and flagellate with a distinct apical seta, legs with tarsus and tibia sometimes fused or delimited only by a
suture, with three rows of spines within the ovisac band. *Mixorthezia* is distributed throughout the Neotropical Region.

*Mixorthezia kozari* Vea & Grimaldi sp.n.

(Figures 2.7A, B, 2.8)

*Types.* Holotype. Complete adult female, with ovisac bearing nymphs, AMNH DR-14-310, American Museum of Natural History. Paratypes. A juvenile or young female, AMNH DR-15-9; adult female with ovisac, AMNH DR-JVe200. Type locality and horizon. Miocene of the Dominican Republic.

*Description.* Adult female. Body pear-shaped, dorsoventrally flattened, head narrow with greatest width on first abdominal segments, 0.81 mm long, 0.76 mm wide (ovisac and wax secretion: 1.58 mm long and 1 mm wide). Antennae 4-segmented, inserted ventrally at frontal margin, distance between antennae 93 µm, with slightly clavate apical segment; approximate antennal length 0.38 mm. Segmentation length in µm: first segment 70 long, second segment 45, third segment 135, apical segment 124; with short, hair-like setae, last segment with a long, hair-like, apical seta, 167 µm, a subapical seta 62 µm and a flagellate sensory seta. Eyestalk protruding. Mouthparts visible, labium narrow, 2-segmented, about 150 µm long. Legs well developed and strong. Leg segment lengths, in µm: coxa ca 136; trochanter and femur (fused) 302; tibia 62, with 3–4 rows of spinose setae; tarsus 185, with 10–12 rows spinose setae, both segments faintly separated and with same diameter as tibia; sensory setae visible, without digitules; claw 25 µm long, without denticles, with hair-like digitule at base. Wax covering made transparent by preservation in amber, completely covering dorsum; with eight pairs marginal lobes,
Figure 2.7. Photomicrographs of *Mixorthezia* spp., *Nipponorthezinella* sp. and *Newsteadia* sp. in Miocene amber from the Dominican Republic. A–C. *M. kozari* Vea & Grimaldi sp.n., A, B. holotype, in ventral view, using transmitted and reflected light. A. and just transmitted light to show eggs and nymphs in ovisac (B), C. *M. dominicana* Vea & Grimaldi sp.n., in dorsal view. The holotype specimen is suspended in the amber on a sheet of fungal mycelia, B. *Nipponorthezinella* sp., in dorsal view, E. *Newsteadia* sp., in dorsal view with ovisac including eggs and first-intar nymphs.
Figure 2.8. Drawings of *Mixorthezia kozari* Vea & Grimaldi sp.n. in Dominican amber (holotype). **A.** Dorsal habitus, as preserved, **B.** Ventral habitus, without wax lobes and ovisac, **C.** Detail of mesothoracic leg, **D.** Detail of entire antenna, including eye.
frontal lobe separated from lateral lobes, eighth lobe almost completely covering ovisac, caudal lobe half the length of eighth lobe; with seven rows small, faint separated median and submedian lobes. All wax lobes inclined posteriad. Ovisac well developed, 812 μm long, containing two first-instar nymphs and four eggs in specimen AMNH DR14-310. Adult male unknown.

**Diagnosis.** *Mixorthezia kozari* differs from *M. dominicana* as follows: by the third antennal segment being relatively shorter (35.5% vs. 41% of total antennal length) and the apical seta significantly longer than subapical seta (vs. apical subapical setae of subequal lengths in *M. dominicana*), marginal wax lobes much more developed than submedian and median lobes (vs. marginal wax lobes as developed as submedian and median lobes in *M. dominicana*), and frontal lobes fused (vs. separated).

**Etymology.** The epithet is in recognition of Ferenc Kozár, for his work on Recent Ortheziidae and his major contributions to the current knowledge of this family.

**Mixorthezia dominicana** Vea & Grimaldi sp.n.

(Figures 2.7C, D, 2.9)

Holotype. Complete adult female, AMNH DR19-1 American Museum of Natural History. Type locality and horizon. Miocene of the Dominican Republic.

**Description.** Adult female. Body elongate oval, 1.28 mm long, 0.77 mm wide, dorsoventrally flattened. Antennae 4-segmented, inserted at frontal margin ventrally, distance between antennae 80 μm, with slightly clavate apical segment; approximate antennal length 0.51 mm. Segmental lengths in μm: first segment 111, second segment 50, third segment 210, apical segment 142; with short, hair-like setae, apical segment with hair-like apical seta 142 μm long, subapical seta 99 μm, sensory seta flagellate.
Figure 2.9. Drawings of *Mixorthezia dominicana* Vea & Grimaldi sp.n. in Dominican amber (holotype). A. Dorsal habitus, as preserved, B. Detail of entire right antenna, including eye, ventral view.
Eyestalks protruding. Mouthparts with long, narrow labium, probably 2-segmented, with numerous fine setulae on labium apex. Legs well-developed, slender, segment lengths in µm: coxa ca 111, trochanter fused to femur, both 315; tibia 111, with 3–4 rows of spinose setae; faintly separated from tarsus (315 µm), with 12–15 rows of spinose setae, without tarsal digitule; claw 50 µm long, without denticle and hair-like digitules. Wax lobes well developed but transparent due to preservation; consisting of nine marginal lobes, a frontal lobe barely protruding from body margin, caudal lobe protruding from anal ring. Dorsal wax lobes consist of eight submedian and eight paramedian pairs, all symmetrical and arranged segmentally from head to abdominal segments. Ovisac absent.

Adult male unknown.

Diagnosis. See diagnosis of *M. kozari*

Etymology. The epithet is in reference to the provenance of the amber deposit (Dominican Republic) in which the species was discovered.

Comments. The two new species were attributed to *Mixorthezia* based on the following characteristics: 4-segmented antennae, slightly clavate apical segment; the long, differentiated apical seta on last antennal segment; wax lobes completely covering dorsum; tibia and tarsus of same diameter, separated by a fine suture, and the tarsus significantly longer than the tibia. Species of *Mixorthezia* have a rather elongate labium, as do *M. kozari* and *M. dominicana*. Other cuticular characters were not observable in amber specimens, but the leg and antennal structures seem sufficient to determine the genus. *Mixorthezia kozari* has a remarkably well-preserved, transparent ovisae, through which nymphs and eggs are can be observed. From observable features, the fossil taxa of *Mixorthezia* differ from the Recent ones by the presence of both median and submedian
wax lobes (vs. with submedian and median lobes fused and either covering the whole
dorsum or with only a midline band in Recent Ortheziidae). Similar preservation has been
reported by Koteja & Zak-Ogaza (1988b) for *Newsteadia succini* in Baltic amber.
Another undescribed specimen of *Newsteadia* from Dominican amber in the AMNH
collection has such an ovisac containing visible eggs and nymphs (Fig. 2.7D).

*Summary of described fossil Ortheziidae*

These are listed by original combination and with earliest descriptions first. The
designations ‘Cocc-####’ were numbers assigned by Koteja for specimens he studied.

- *Ochyrocoris electrina* (Menge, 1856). Type, ?female in Baltic amber, apparently
deposited in Albertus University, Königsberg, and presumed lost. Possibly an
*Arctorthezia* sp. *Palaeonewsteadia huaniae* (Koteja, 1987a). Holotype, adult male
in Baltic amber, in Zoological Museum (Dept. of Entomology) of the University
of Copenhagen, Denmark. Collection 03/01/1956 by C.V. Henningsen on the
Jutland Peninsula, Denmark.

- *Protorthezia aurea* (Koteja, 1987b). Holotype, adult male (type no. K 933) in
Baltic amber, in Geologisch-Paläontologisches Institut und Museum der Georg-
August-Universität, Göttingen, Germany. Presumably from the Samland
Peninsula.

- *Arctorthezia antiqua* (Koteja & Zak-Ogaza, 1988a). Holotype, female (Cocc-113)
in Baltic amber, in the Department of Palaeontology, Natural History Museum,
?urticae*, 1965’.


Morphological characters

Below are the descriptions of 69 morphological characters of adult females used in the phylogenetic analysis, coded for 39 exemplar Recent and eight fossil species in amber.

NB: The character state zero (0) does not necessarily indicate the plesiomorphic state.

1. Number of antennal segments (Fig. 2.10A–D): The number of antennal segments varies significantly from 2 to 9 segments; with reduced, 2-segmented antennae occurring in the ground-dwelling *Acropygorthezia williamsi*. Most genera have a constant number of segments, except for *Newsteadia* where it can vary from 3 to 7 segments. States: 0 = two; 1 = three; 2 = four; 3 = five; 4 = six; 5 = seven; 6 = eight; 7 = nine.

2. First antennal segment conspicuously larger than other segments (Fig. 2.10A): *Newsteadia* spp. all have a significantly larger and longer first segment than the other antennal segments. This feature is characteristic of the genus (Miller & Kozár, 2002). States: 0 = no; 1 = yes.

3. Labium segmentation: Koteja (1974a) studied the significance of labium morphology and hypothesized a reduction of labium segmentation across lineages of Coccoidea. In the Ortheziidae and selected outgroups, the number of segments varies from 1 to 2 segments. States: 0 = one; 1 = two.

4. Three setae inserted on one basal socket at the apex of labium: All Ortheziidae have the labium bearing mainly hair-like setae. The Ortheziolinae are characterized by the presence of three setae inserted on one basal socket (Kozár, 2004). States: 0 = no; 1 = yes.
Figure 2.10. Photomicrographs of antennal, leg details of exemplars of Ortheziidae and some characters used in the phylogenetic analysis, from slide-mounted specimens. Antennae (scale bars = 100 µm): A. Newsteadia floccosa with long and hair-like apical seta, long 1st segment, B. Ortheziolacoccus anazoboeensis with the developed pseudobasal segment and eye fused to antenna, C. Nipponorthezia obscura with partly developed pseudobasal segment, D. Orthezia cacticola with short and stout apical seta. Legs (scale bars = 100 µm): E. Newsteadia floccosa, with fused tibia and tarsus, F. Orthezia newcomeri, with fully separated tibia and tarsus, G. Nipponorthezia obscura, with tibia and tarsus separated by a fine suture. Character details (scale bars = 50 µm or otherwise indicated), H. Orthezia urticae, enlarged spines between tibia and tarsus, I. Mixorthezia reynei, sensory pore between tibia and tarsus (arrow), scale bar = 25 µm, J. Ortheziola vejdovskyi, sensory seta between tibia and tarsus (arrow), K. Nipponorthezinella guadalcanalia, microseta on last antennal segment (antenna), L. Orthezia urticae, thoracic spiracles with bands of spines, M. Arctorthezia cataphracta, thoracic spiracles with groups of pores, N. Newsteadia minima, tubular ducts between wax spines, scale bar = 25 µm, O. Ortheziola vejdovskyi, thumb-like pores, scale bar = 25 µm.
5. Stiff setae on second segment (Figs 2.3, 2.4): The presence of stiff setae on the second segment is a probably a diagnostic feature of *Burmorthezia*. States: 0 = absent; 1 = present.

6. Cephalic plate on dorsal surface of head: This feature is present and diagnostic of *Praelongorthezia*. ‘Sclerotic plates’ (Kozár, 2004: 318) are present in *Insignorthezia pseudinsignis* but appear different in shape and are represented in two rows on the head. States: 0 = absent; 1 = present.

7. Number of tarsal segments. Most of female Coccoidea have one tarsal segment although a few families can have two (usually the first tarsal segment is reduced), as in one selected outgroup, *Matsucoccus gallicolus*. States: 0 = one; 1 = two.

8. Pseudobasal antennal segment (Figs 2.10B, C, 2.11F, G): Some genera possess an additional structure on the antenna called the pseudobasal segment, which occurs at the base of the first segment. It is identified relative to the position of the second segment, which bears the Johnston’s organ. In some genera the pseudobasal segment fuses the eyestalk with the antenna (e.g. Orthezioliinae). A few species that have this segment also have the eye separated from the antenna (e.g. Mixortheziini and Nipponortheziini). States: 0 = absent; 1 = well developed; 2 = weakly developed.

9. Eye fused to antennal base (Figs 2.10B, 2.11F): Fusion of the eye to the antennal base is found in some genera and is generally accompanied by the presence of the pseudobasal segment. States: 0 = no; 1 = yes.

10. Differentiated setae on last antennal segment: The family Ortheziidae is defined traditionally in part by large, differentiated setae on the apex and subapex of the terminal segment. All extant members of the family possess differentiated setae, as
Figure 2.11. Drawings of morphological details discussed for the character matrix (not to scale): A. Long antennal apical seta, B. Short antennal apical seta, C. Labium showing a narrow apical segment, D. Labium showing elongated apical segment as broad as the rest of labium, E. Base of antenna without pseudobasal segment and eye separated from antenna, F. Base of antenna with a developed pseudobasal segment and eye fused to it, G. Base of antenna with a pseudobasal segment with eye separated from it, H. Tibia separated from tarsus with two spines on tibia, with claw denticle, I. Tibia and tarsus separated with a cuticular suture, without claw denticle, J. Straight leg setae, K. Curved leg setae, L. Sensory seta on tibia, M. Microseta on last antennal segment.
opposed to the fossil ortheziids in Cretaceous amber, and our outgroups, which lack them. States: 0 = absent; 1 = present.

11. Length of differentiated apical seta (Figs 2.10A, D, 2.11A, B): When there is a differentiated apical seta on the last antennal segment, the seta can be short especially in the Ortheziinae and long in the rest of the Ortheziidae. States: 0 = short (<one quarter of last antennal segment length); 1 = long (>one quarter of last antennal segment).

12. Type of differentiated apical seta: In addition to the seta, the apical seta varies in type. There can be a stout type (usually short) and a fleshy type (usually long). States: 0 = stout; 1 = fleshy.

13. Flagellate sensory seta on terminal segment (Figs 2.8, 2.11A): A sensory seta is often present on the apical segment as a stout seta with a rounded, blunt tip. It can also be long, slender, and tapered. Usually, the shorter sensory seta is found in genera that also bear a short, stout apical seta. States: 0 = absent; 1 = present.

14. Type of unspecialized setae on antenna (Figs. 2.3, 2.4, 2.8): Excluding the flagellate sensory seta, and the apical and subapical setae, all others on the antenna are the unspecialized setae. They are usually the same shape along the antenna but vary in number among segments and genera. Usually the first and second segments bear fewer setae. States: 0 = hair-like; 1 = spine-like.

15. Unspecialized antennal setae: States: 0 = straight; 1 = curved.

16. Subapical seta on terminal segment (Fig. 2.10A, B): The apical seta usually is accompanied by a subapical one, and is longer than the unspecialized setae. States: 0 = absent; 1 = present.
17. Longest antennal segment: Length of segment is variable across the family. If there are more antennal segments, the first or second one tends to be the longest; with fewer segments (3 to 6), one of the segments becomes the longest one. This suggests that loss of segments involves the fusion of some intermediate segments. States: 0 = first segment; 1 = second segment; 2 = segment between the second and the terminal one; 3 = apical segment.

18. Dimensions of first antennal segment: The proportions of the first segment vary across the family and can be informative for generic identification. In Newsteadia, it is usually longer than wide; in Orthezia it is nearly square. States: 0 = width > length; 1 = length > width; 2 = square.

19. Shape of first antennal segment: Most ortheziids possess a straight antennal segment; a few possess curved ones, which can be informative for identification although this state is not characteristic of one group. States: 0 = straight; 1 = curved.

20. Shape of terminal antennal segment (Fig. 2.11A, B): The shape of the apical segment occurs in two states; genera with long apical setae tend to have the apical segment slightly clavate, as opposed to genera possessing a short, stout apical seta, which tend to have a terminal segment of uniform thickness. States: 0 = filiform; 1 = clavate.

21. Microseta on apex of terminal antennal segment (Figs. 2.10K, 2.11M): a minute microseta can occur at the tip of the antenna adjacent to the apical seta. Although not exclusive of one group, Mixorthezinii bear obvious microsetae and Neomixorthezia Kozár has characteristic microsetae with tips that are slightly blunt. States: 0 = absent; 1 = present.
22. Number of undifferentiated setae on terminal antennal segment: In the Ortheziidae, antennal structure seems to correlate with the number of undifferentiated setae. For instance, antennae with short, stout apical setae always have very few undifferentiated setae. States: 0 = less than 20; 1 = 20–60; 2 = more than 60.

23. Eye shape: Morrison (1925) illustrated well the diversity of eye shape in the Ortheziidae. Two types of eyes are defined here: a sessile eye (Fig. 2.11E), a stalked, protruding eye (Fig. 2.11F). States: 0 = sessile; 1 = stalked; 2 = absent.

24. Femur and trochanter: In those families of Coccoidea that have well-developed legs, the femur and trochanter are separated. In the Ortheziidae, the femur and trochanter are fused except for Arctorthezia. Species from the Cretaceous possess an (assumed plesiomorphic) unfused femur and trochanter. States: 0 = unfused; 1 = fused.

25. Tibia and tarsus (Figs. 2.10E–G, 2.11H, I): Within the Ortheziidae, the tibia and tarsus either can be fully separated, in which case the tibia is larger in diameter than the tarsus; or largely be fused but with a fine suture between the segments; or completely fused, in which the tibia and tarsus can be delineated only by the presence of a sensory seta and/or sensory pore at the limit between the tibia and tarsus. States: 0 = distinctly separated (tarsus being less wide than tibia) (Figs. 2.10F, 2.11H); 1 = separated by a fine suture (Figs 2.10G, 2.11I); 2 = fused (no suture present) (Fig. 2.10E).

26. Articulation between tibia and tarsus: when not fused, an articulation is fully developed between the tibia and tarsus. In this analysis it applies only to the outgroup taxa. States: 0 = no; 1 = yes.
27. Enlarged spines between tibia and tarsus (Figs. 2.10H, 2.11J): when the tibia and tarsus are separated fully, a pair of long, stout spines is present on the ventral side of the leg. States: 0 = no; 1 = yes.

28. Ratio of length of tibia and tarsus: in other coccoid families the tibia is usually longer than the tarsus. In the Ortheziidae, two trends are observed: the *Orthexia*-like genera, in which the tibia is longer than the tarsus, and the *Newsteadia*-like genera, with the tarsus longer than the tibia. States: 0 = tibia longer than tarsus; 1 = tarsus longer than tibia.

29. Claw digitule: the digitule is a seta-like structure inserted at the base of the claw. In the Ortheziidae they can be spine-like or hair-like. States: 0 = hair-like; 1 = spinelike; 2 = clavate.

30. Claw denticle (Fig. 2.11H): the claw ventrally can bear small teeth called denticles. One or more may be present. States: 0 = absent; 1 = present.

31. Setae on tibia and tarsus: setae are present always on the tibia and tarsus, which can be all spine-like (spiniform) or all hair-like (setiform), but in some species they are setiform except for spiniform setae on the ventral side of the tarsus. States: 0 = all setiform; 1 = all spiniform; 2 = spiniform ventrally and setiform dorsally.

32. Leg setae (Fig. 2.11J, K). States: 0 = straight; 1 = curved.

33. Number of rows of setae on tarsus: setae on the tibia and tarsus are arranged in rows, which can vary in number. States: 0 = less than 5 rows; 1 = between 6 and 9; 2 = more than 10.
34. Number of sensory pores on trochanter: the trochanter always possesses 3 or 4 sensory pores basally. States: 0 = 3 pores; 1 = 4 pores; 2 = more than 4 pores; 3 = 2 pores.

35. Sensory seta between tibia and tarsus (Figs. 2.10J, 2.11L): this seta is usually present even when the tibia and tarsus are fully fused, with or without a fine suture delineating them. As such, the sensory seta along with the sensory pore (character 26) allows delineating the tibia from the tarsus. States: 0 = absent; 1 = present.

36. Sensory pore between tibia and tarsus (Figs. 2.10I, 2.11H, I): This sensory pore is present at the proximal end of the tibia. States: 0 = absent; 1 = present.

37. Strong spines on coxa: the coxa usually bears a few setae of the same type as found on the trochanter and femur, but in some cases additionally it can have distinctly short, stout spines (e.g. *Newsteadia monikae*). States: 0 = absent; 1 = present.

38. Apical segment of labium (Fig. 2.11C, D): even within the genus *Newsteadia*, the labium shape can vary significantly (Kozár, 2004: 32). In the family, the apex of the labium can be narrow or broad. States: 0 = almost as broad as base and not elongate; 1 = narrow; 2 = long, with apex almost as broad as base.

39. Thumb-like pores (Fig. 2.10O): these are conical pores found in clusters around the anal ring (Kozár & Miller, 2000). They are found in the Ortheziolinae. States: 0 = absent; 1 = present.

40. Quadrilocular pores on dorsum: these pores are characteristic of the family and form tube-like or pore-like structures with four loculi and can vary in detailed structure (Kozár, 2004). On the dorsal surface, they occur among the wax spines. States: 0 = absent; 1 = present.
41. Trilocular pores: these pores are found specifically in the Pseudococcidae and Putoidae and are defined by pores with three loculi arrangement in a swirled manner and produce the wax. States: 0 = absent; 1 = present

42. Tubular ducts without ductule (Fig. 2.10N): in the Newsteadiinae, tubular ducts are found among the wax spine lobes, but they possibly are modified quadrilocular pores that have become extended in length. States: 0 = absent; 1 = present.

43. Ovisac band: the adult female ortheziid is recognizable by its large ovisac, in which the eggs and/or nymphs are brooded. On a microscopic level, the presence of the ovisac is obvious by the presence of an ovisac band on the ventral surface of the abdomen, delineated by a thick line of wax spines. The band is generally not visible in amber specimens, because the surface is obscured by wax, although the ovisac can be macroscopically obvious. States: 0 = absent; 1 = present.

44. Spines in ovisac band: in most ortheziids, the inner surface of the ovisac band possesses rows of spines. In some cases these are absent (e.g. most Newsteadia species). States: 0 = absent; 1 = 2 or less; 2 = more than two.

45. Number of loculi on pores of venter of last abdominal segments (within the ovisac band): the inner surface of the ovisac also bears simple and multilocular pores. For the multilocular pores, the number of loculi varies. States: 0 = >10; 1 = 5–10; 2 = <5.

Characters 46–53. Abdominal spiracles: the Ortheziidae has been classified as an archaeococcoid group by the presence of abdominal spiracles, which are absent in the neococcoids. Within the family the number of abdominal spiracles as well as the arrangement varies. For instance, Newsteadia has five abdominal spiracles, arranged consecutively and the first spiracle starts on the first abdominal segment; Ortheziolia
has four abdominal spiracles, but the first three spiracles are consecutive and the fourth one is found near the anal ring (Miller & Kozár, 2002).

46. Abdominal spiracle 1: 0 = absent; 1 = present.
47. Abdominal spiracle 2: 0 = absent; 1 = present.
48. Abdominal spiracle 3: 0 = absent; 1 = present.
49. Abdominal spiracle 4: 0 = absent; 1 = present.
50. Abdominal spiracle 5: 0 = absent; 1 = present.
51. Abdominal spiracle 6: 0 = absent; 1 = present.
52. Abdominal spiracle 7: 0 = absent; 1 = present.
53. Abdominal spiracle 8: 0 = absent; 1 = present.

54. Position of abdominal spiracles: the abdominal spiracles can be present on the ventral or dorsal surface. In some genera, they are present on both surfaces, anterior abdominal spiracles being on the ventral surface and last two posterior abdominal spiracles found on the dorsal surface (e.g. *Orthezia* spp.). States: 0 = ventral; 1 = dorsal; 2 = both.

Characters 55–62: wax lobes are defined using slidemounted specimens as plates or areas of dense minute spines on the surface of cuticle (Figs. 2.1A–D, 2.12). The dorsal wax plates have been divided as followed: submedial dorsal wax plates are adjacent to the marginal wax plates, the median wax plates are found medially, from the head to the abdomen. Figure 2.12 represents the variation of dorsal wax plate distribution across the Ortheziidae. When wax plates are absent, all related characters are coded as non-applicable (‘-’).
Figure 2.12. Representations of dorsal wax plate distribution across the Ortheziidae: 
A. Submedian plates present and unfused from median plates, B. Submedian plates present on abdominal segments only, C. Submedian plates fused to median plates, D. Submedian plates absent, E. Triangular midline plates.
55. Dorsal wax lobes: on the dorsum, wax lobes can cover the whole surface, which is the case for instance in *Arctorthezia* spp. In other cases, the dorsal wax lobes do not completely cover the dorsum. States: 0 = completely covering the dorsum (Fig. 12C, E); 1 = partially covering the dorsum (Fig. 2.12A, B, D); 2 = absent.

56. Submedian dorsal wax lobes. States: 0 = absent (Fig. 2.12D); 1 = present and well separated from median plates (Fig. 2.12A); 2 = fused to median dorsal plates (Fig. 2.12C, E); 3 = present on abdominal segments only (Fig. 2.12B).

57. Submedian dorsal wax lobes divided segmentally: States: 0 = no; 1 = yes.

58. Circular pore clusters: the clusters of pores (Morrison, 1952) are found on the dorsal surface at the upper corners of the marginal plates, separating the submedian and marginal plates. This feature is characteristic of *Arctorthezia pseudoccidentalis* but was discovered also in *Arctorthezia baltica* Vea & Grimaldi sp.n. States: 0 = absent; 1 = present.

59. Ventral wax secretion on thorax: wax secretion on the venter is usually present as plates of secretion rather than lobes. In some cases it doesn’t completely cover the surface. For mounted specimens, wax presence was coded through the distribution of wax spine plates. States: 0 = absent; 1 = completely covering the ventral surface; 2 = weakly present compared to dorsum; 3 = present with holes on marginal thoracic segments.

60. Number of marginal wax lobes: the number of marginal wax lobes varies across the Ortheziidae. The count here was made by including the frontal and posterior marginal lobes. States: 0 = 8 lobes; 1 = 9 lobes; 2 = 10 lobes; 3 = 11 lobes; 4 = wax plates not well separated.
61. Median wax lobes (Fig. 2.12): the median wax plates are often fused to the submedian plates but sometimes they are absent, resulting in a medial naked area on the dorsum. Here, the median wax plates have been distinguished from the midline asymmetrical wax lobes found in *Arctorthezia*. States: 0 = absent; 1 = present.

62. Dorsal midline triangular wax lobes (Fig. 2.12E): in *Arctorthezia*, a triplet of triangular or shield shaped wax lobes are present on the dorsum of the thoracic segments. States: 0 = absent; 1 = present.

63. Thoracic spiracle pores (Fig. 2.10M): pores of different types can be present around the thoracic spiracles. States: 0 = no pores; 1 = pores with 4 loculi; 2 = pores with a small middle spine; 3 = pores with more than 4 loculi.

64. Band of spines around thoracic spiracles (Fig. 2.10L): the Ortheziinae is characterized by the presence of a band of spines around the spiracles. States: 0 = absent; 1 = present.

65. Wax lobes inclined anteriad: wax covering was not used in this study except for the orientation of some anterior wax lobes that are inclined anteriad, a distinctive feature of the genus *Newsteadia*. Access to more fresh and/or dry material would enable a comparison of wax coverings with the fossil specimens. Photographs of specimens in their natural state would be the most informative as the wax covering is damaged when the specimen is conserved dry or in alcohol. States: 0 = no; 1 = yes.

66. Anal ring: the Ortheziidae and other families (e.g. Pseudococcidae) have an anal ring often bearing three pairs of setae and secretion pores. States: 0 = absent; 1 = present.

67. Setae on anal ring: the length of setae on the anal ring varies according to genera. Some genera have relatively short setae, which are usually spine-like (e.g.
Newsteadia) and the genera with long setae will be hair-like or fleshy (e.g. Orthezia). States: 0 = length > longitudinal diameter of anal ring; 1 = length < longitudinal diameter of anal ring.

68. Lateral seta of anal ring: the lateral pair of setae on the anal ring are usually of the same length as the anterior and posterior setae but in the Nipponortheziini, the lateral pair is at least half the size of the other setae and hair-like as opposed to spine-like. States: 0 = same length as the other anal ring setae; 1 = significantly shorter than the other anal ring setae.

69. Sclerotized plate anterior to anal ring: in Ortheziolinae the anterior portion of the anal ring has a sclerotized cuticular plate, which seems to be characteristic of this subfamily. States: 0 = absent; 1 = present.

*Phylogenetic relationships and classification*

The parsimony analysis resulted in 173 most parsimonious trees (L = 293 steps); the strict consensus tree is presented in Fig. 2.13. The family Ortheziidae was retrieved as a monophyletic group. *Acropygorthezia williamsi* was retrieved as the sister group to all Ortheziidae + Burmorthezia. This recently described species lives in subterranean ant nests, and both sexes have reduced features, including a loss of the wax secretions. The adult female lacks an ovisac, lacks an anal ring with three pairs of setae and pores and has two sensoria on the trochanter (in contrast to other Ortheziidae that have three or four such sensoria). From the original description, *A. williamsi* has been attributed to the Ortheziidae based on the presence of quadrilocular pores, dome-shaped setae, and numerous spines (LaPolla *et al.*, 2008); the last of these characters seem to be highly modified versions of the wax spines typical of the family. The spines are more spiniform
Figure 2.13. **Strict consensus of the 173 most parsimonious trees obtained from TNT analysis.** L = 293 steps; RI = 0.73; CI = 0.34. Unambiguous character changes were mapped using Winclada (Nixon, 2002). Black circles show synapomorphies or autapomorphies, white circles show homoplastic characters. Character numbers are indicated above circles as referred in the text. Bootstrap support 20% is indicated at each node. Coloured bars indicated each tribe and colour code corresponds to the different subfamilies. Paraphyletic groups are shown in quotes.
and without a rounded apex in *A. williamsi* (in contrast to the more rounded apex in the rest of ortheziids; see Morrison (1925) for detailed drawings of wax spines). The absence of numerous features typical of the Ortheziidae in *Acropygorthezia* resulted in a high percentage of inapplicable characters in the morphological matrix. This probably explains the placement of *A. williamsi* as the sister group of the rest of the Ortheziidae. This is the only species attributed to the Ortheziidae with significantly reduced features, due to the obligate symbioses with ants and subterranean habitat. Therefore, our results do not support with certainty the placement of this species. The analysis excluding *Acropygorthezia williamsi* did not affect substantially the relationships that were found previously. Although fewer most parsimonious trees (12) were found the strict consensus tree did not resolve the node of *Burmorthezia* + rest of the Ortheziidae and decreased the resolution of the Ortheziinae (Figure S2.1). Bootstrap values were generally higher when excluding *A. williamsi* and this can be explained by the presence of numerous autapomorphies (due to reductions of morphological structures) for this species. In fact, the presence of autapomorphies negatively affects the bootstrap (Carpenter, 1996).

*Burmorthezia* is the sister group to the rest of the Ortheziidae and is defined on the basis of a separated trochanter and femur (character 24; plesiomorphic state), undifferentiated apical setae on the last antennal segment (character 10; plesiomorphic state) with two stiff setae on the second segment (character 5), and a distinctly separated tibia and tarsus (similar to the Ortheziinae), with the tibia longer than the tarsus (plesiomorphic state). Even if we did not code characters that are known to vary between nymphs and adults, this genus is only represented by second-instar nymphs, and the relationships retrieved in this study could be partly caused by nymphal characters. *Burmorthezia* is an extinct sister
group to a monophyletic crown group comprising the Recent and Tertiary Ortheziidae. *Burmorthezia* shares with crown group Ortheziidae the distinctive nature of wax secreted into bundles or lobes, a large eye lens situated on a long eye peduncle, and the general morphology of the leg. *Cretorthezia* sp. in Lebanese amber (Koteja & Azar, 2008) also has the trochanter and femur separated as in *Burmorthezia*, as well as undifferentiated antennal setae, but *Cretorthezia* sp. differs from *Burmorthezia* in bearing many more wax lobes. Unfortunately, *Cretorthezia* sp. could not be included in the analysis because of a lack of critical characters in the original description (most cuticular microstructures were obscured by wax), and because the description could not be verified as the unique specimen seriously deteriorated soon after description. Additionally, Koteja & Azar (2008) described the genus based on a male specimen and hypothetically assigned the apterous form (which he supposed to be a young female or an immature) to this genus. Only information such as occurrence in the same piece of amber or in *copula* specimens could support this hypothesis. Cladistically, it is likely that *Burmorthezia* should be assigned to a new family sister to the Ortheziidae even if it was described based on immatures, in which case *Cretorthezia* should also be in another new family. However, in our view, this leads to a proliferation of family names, unwarranted in lieu of data on cuticular microstructures. The subfamilies Newsteadiinae, Ortheziolinae and Ortheziinae are each a monophyletic group (discussed individually below), thus largely confirming Kozár’s classification, although our analysis supports the paraphyly of the Nipponortheziolinae.
Subfamily Newsteadiinae

The subfamily Newsteadiinae is sister group to the Nipponortheziolinae + Ortheziolinae. The Newsteadiinae is defined by a first antennal segment conspicuously larger than other antennal segments (character 2), dorsal wax lobes protruding forward (character 65), tubular ducts on the dorsum between the wax spines (character 42), and the absence of a band of spines inside the ovisac band on the venter (character 44). This subfamily includes only the genus *Newsteadia*, which has the most species in the Ortheziidae. Since the revision by Morrison (1925, 1952), the known diversity of the genus has increased from 11 to 57 species, with the main contributions coming from a series of papers (Kozár & Konczné Benedicty, 1999, 2000, 2001; Miller & Kozár, 2002) in which all geographic regions were covered. The tubular ducts characteristic of the genus can vary in length across the genus but always have four loculi. Therefore, they could be modified dorsal quadrilocular pores. *Newsteadia* has been defined for some time as a distinct lineage of the Ortheziidae, based on morphology of the mouthparts and comparative study of *Newsteadia* and *Orthezia*. Koteja (1974b) observed that *Newsteadia* and *Ortheziola* differed from the *Orthezia* group based on the antennae and legs of the female, with *Newsteadia* and the Ortheziolinae having a long, hair-like apical seta on the apical antennal segment, the tibia and tarsus fused or only partly separated by a fine suture, and a tibia shorter than the tarsus. Although only one adult male, that of *Newsteadia floccosa* (De Geer) has been described and illustrated, Koteja concluded that *Newsteadia* is a ‘more specialized’ genus than *Orthezia* (Koteja, 1986). Our analysis supported that *Newsteadia* is a distinct lineage from the Ortheziinae (in which *Orthezia* is included), and is more related to the other genera of the Ortheziidae than the Ortheziinae.
Additional knowledge of male morphology of the Ortheziolinae and Nipponortheziinae would allow confirmation of these relationships. To date, other adult males of Ortheziidae are available but undescribed and only include representatives of the subfamily Ortheziinae. The fossil *Newsteadia succini* from Baltic amber is closely related to the Recent species. *Newsteadia* has unusual variability in the number of antennal segments (from 3 to 8), in comparison to all other genera of the Ortheziidae. *Newsteadia succini* possesses four antennal segments, with a long, hair-like apical seta on the last segment, and it possesses wax lobes inclined anteriad but, according to Koteja & Zak-Ogaza (1988b), the tibia and tarsus are not fused and the leg has a ‘clear transverse tibiotarsal fold’. The analysis retrieved *N. succini* as sister group of all the sampled *Newsteadia*, allowing us to assign a minimum age of the genus at 43 Ma.

**Subfamily Ortheziinae**

The subfamily Ortheziinae is the other distinct lineage retrieved in our analysis, and one which has been noted previously by other coccidologists. The monophyly of this subfamily is well supported by the distinctive short, stout apical seta on the terminal antennal segment (character 5), the separated tibia and tarsus, and the presence of two enlarged spines on the tibia (character 19). The tarsus is more constricted in diameter than the tibia. Kozár (2004) defined two tribes within the Ortheziinae, the Arctortheziini and the Ortheziini. Here, *Arctorthezia* and the Orthezinii are unresolved nodes. The Arctortheziini only comprises the genus *Arctorthezia*, which has four extant and three fossil species (two described here). Although the genus is easily recognizable by its triplet of triangular or shield-like midline wax lobes on the dorsum, the optimization of this character (62) in the consensus tree suggests that the appearance of the midline wax
lobes is a synapomorphy of the subfamily Ortheziinae, which was lost subsequently in the tribe Ortheziini. Observations of slide-mounted specimens indicate that most extant *Arctorthezia* do not have the trochanter and femur completely fused and have seven or eight antennal segments. The original description of *Arctorthezia antiqua* indicated that the ‘base of eye stalk obscured, but the apex seems to bear numerous (about 12) ommatidia. This feature is so curious that we must wait with its interpretation until more material has become available’ (Koteja & Zak-Ogaza, 1988a: 44). Study of the type specimen in the BMNH, London, by one of us (I.V.), did not find conclusive evidence for these multiple ommatidia, the specimen being heavily occluded by a layer of debris. The newly discovered adult females of *Arctorthezia* in Baltic amber reported here do not have eyes with multiple ommatidia, but have a single lens typical of the family. *Arctorthezia* is another lineage that was well established by at least 43 Ma. Based on the fact that fossil specimens are covered with a layer of fine particles, apparently from soil and leaf litter, *Arctorthezia* seems not to have changed its habits over this time period, as all current species generally are collected in leaf litter. The tribe Ortheziini is monophyletic, defined by the presence of a fused trochanter and femur (character 24), the tibia and tarsus bearing hair-like setae dorsally and spine-like setae ventrally (character 31), the triplet of triangular midline wax lobes absent (character 62), and the thoracic spiracle without pores (character 63). The tribe was recognized by Kozár (2004) for the genera *Orthezia*, *Graminorthezia*, *Praelongorthezia* and *Insignorthezia* Kozár. The strict consensus of our analysis did not resolve the relationships within this tribe. The Ortheziini have colonized plants, in contrast to Arctortheziini, which may be saprophagous. Species of *Orthezia* are
polyphagous, *Graminorthezia* mostly feed on Poaceae (grasses) in the New World, and *Insignorthezia* feed on woody plants.

‘*Nipponortheziiinae*’

Our analysis did not support the monophyly of the Nipponortheziiinae. The tribe Mixortheziini, as defined by Kozár (2004), comprising the *Jermycoccus* Kozár & Koncúné Benedicty, *Mixorthezia* and *Neomixorthezia*, is supported as monophyletic, defined by four-segmented antennae (character 1), spine-like unspecialized antennal setae (character 14), and anal ring setae shorter than the longitudinal length of the anal ring (character 68). *Jermycoccus* is the living sister-group to the rest of the Mixortheziini. *Jermycoccus* is monotypic and has a peculiar morphology compared to the rest of the Ortheziidae. Its dorsum is covered with small groups of wax spines, each group usually with 3–5 spines, a long seta, and one quadrilocular pore (Kozár & Koncúné Benedicty, 2002). We found *Mixorthezia* to be the sister group to *Neomixorthezia*, the grouping defined by a partially developed pseudobasal segment (character 8), to which the eyestalk is not attached (character 9). The species in Dominican amber unequivocally are *Mixorthezia*, indicating that this lineage was fully established at least 17 Ma. The Nipponortheziiini is a paraphyletic group but the lineage including *Nipponorthezia* and *Nipponorthezinella* is well supported by dorsal submedian wax lobes present only on the abdominal segments (character 56), pseudobasal antennal segments not distinctively separated (character 8) and a clavate last antennal segment. The fossil of *Nipponorthezinella* is found sister to the recent *Nipponorthezinella guadalcana*lia, which allows the assignment of this node at a minimum age of 17 Ma. *Neonipponorthezia* was retrieved as the sister group to the Ortheziolinae + Mixortheziini lineage. The
Nipponortheziinae is retrieved as paraphyletic as the subfamily Ortheziolinae appears to be sister-group to the included tribe Mixortheziini. To retain a monophyletic subfamily Nipponortheziinae, the Ortheziolinae is reduced in rank to tribe Ortheziolini. The tribe comprises *Matileortheziola* Kozár & Foldi, *Ortheziolacoccus* Kozár, *Ortheziolamameti* Kozár and *Ortheziola* Šulc. Because Kozár (2004) designated a tribe for each of these genera (with only *Ortheziola* in Ortheziolini), all the tribes Matileortheziolini, Ortheziolacoccini and Ortheziolamametini of Kozár become junior synonyms of Ortheziolini (syn.n.).

_Subfamily Ortheziolinae_

The Ortheziolinae is composed mainly of recently described species, or species placed formerly in the genus *Ortheziola* and transferred recently to new genera. This subfamily is clearly monophyletic but is imbedded within the Nipponortheziinae. It bears distinctive autapomorphies, including a well-developed pseudobasal segment at the base of the antenna, to which the eye is fused (characters 8 and 9); three setae inserted in one basal socket on the labium apex (character 4); the presence of a sclerotized plate anterior to the anal ring (character 70); thumb-like pores (character 40) on each side of the anal ring; the thoracic spiracle surrounded by multilocular pores with more than four loculi (character 63) and a claw digitule that is mostly setiform (except in *Matileortheziola*, and in contrast to the rest of the Ortheziidae, which are spine-like). There are no fossil Ortheziolinae. The present distribution includes the Afrotropical, Oriental and Palaeartic regions (Kozár, 2004).
Conclusion: Ortheziid Evolution

The fossil record of Ortheziidae is sparse, being preserved in just four deposits of amber from the Dominican Republic, Baltic Region, Myanmar and Lebanon. However, this geographic coverage is broad, the ages of the deposits cover more than 110 Ma (17, 43, 98, and 125 Ma, respectively); and the phylogenetic positions of the fossil species are both unambiguous and likewise spread across the phylogeny of the family. Thus, inference on lineage chronology can be made. The Cretaceous genera *Burmorthezia* and *Cretorthezia* clearly are stem groups to the Recent and Tertiary ortheziids. One cannot prove the absence of more derived lineages of Ortheziidae in the Cretaceous but, given the rarity of fossil ortheziids in general, the probability that the only three species from the Cretaceous would be plesiomorphic stem groups based on chance alone appears to be extremely remote. It is reasonable to conclude that stem-group Ortheziidae predominated in the Cretaceous. Based on the presence of definitive *Newsteadia* and *Arctorthezia* species in the Eocene, it is also likely that some divergence of early, crown-group lineages took place in the Late Cretaceous, although the diversification of Recent Ortheziidae appears to have occurred largely in the Tertiary. Phytophagy on the shoot system of plants is probably a recently derived feeding mode in the Ortheziidae, largely confined to the monophyletic tribe Ortheziini. The rest of the lineages instead retained a ground-dwelling lifestyle. However, additional and more accurate information about their biology is required to test this hypothesis. There are no fossil Ortheziini, but the relationship of the tribe with Arctortheziini and the Eocene evolution of the latter (evidenced by fossil *Arctorthezia* in Baltic amber) suggest ortheziine divergence took place in the latter half of the Tertiary. The present results contradict the view that
Ortheziidae are a ‘primitive’ family, possibly even the living sister group to the rest of the Coccoidea, and that the Recent Ortheziidae are ancient and relict. A likely explanation, and one already posed (Koteja, 1974b; Danzig, 1980), is that Ortheziidae did not significantly diversify until the Tertiary, when some groups of the family could have evolved onto living on aerial parts of plants independently from other Coccoidea.

Supporting Information

Appendix A Table S2.1. Data matrix for Ortheziidae and outgroups. Please note: Neither the Editors nor Wiley-Blackwell are responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Appendix A Figure S2.1. Strict consensus of the 12 most parsimonious trees retrieved from TNT using the original dataset excluding Acropygorthezia williamsi.

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References


CHAPTER III

MORPHOLOGY OF THE MALES OF SEVEN ORTHEZIIDAE SPECIES (HEMIPTERA: COCCOIDEA)

(To be submitted to American Museum Novitates)

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Abstract

Because adult male Coccoidea rarely live more than three or four days, they are seldom collected and their morphology has been little studied. The systematics of the Coccoidea, therefore, is dependent on the morphology of the paedomorphic adult female. A good example is the family Ortheziidae, in which the males of only four extant and three fossil species are known for more than 200 species. The present chapter is an advance in the study of Ortheziidae, providing descriptions of the morphology of seven described species: Graminorthezia graminis (Tinsley), Insignorthezia insignis (Browne), Newsteadia americana Morrison, Orthezia annae Cockerell, Orthezia graminicola Morrison, Orthezia newcomeri Morrison and Praelongorthezia praelonga (Douglas). The males of three additional genera are known, which provides significantly better sampling of male morphological variation in this family. Variation among genera confirms the latest classification of Kozár, in which Graminorthezia, Insignorthezia and Praelongorthezia are separated from Orthezia. The utility of confocal microscope for the study of uncleared slide preparations is shown to allow better visibility of macrostructures, although minute structures such as pores could not be observed. An identification key to the species of known male Ortheziidae is included.
Introduction

The Ortheziidae or ensign scales insects are a relatively small family of 206 species (Miller et al., 2013) that are mostly found in leaf litter, although some species occur on the upper parts of their hosts and are then often destructive plant pests in greenhouses. The family has an almost worldwide distribution but is, perhaps, most abundant in the Neotropical regions. Kozár (2004) recently revised the Ortheziidae where he defined several new genera and classified its members into new tribes, all based on the adult females. Like all families within the Coccoidea, each species is diagnosed on the basis of female morphology (Morrison, 1925; Morrison, 1952; Kozár and Konczné Benedicty, 2000; Kozár and Miller, 2000; Konczné Benedicty and Kozár, 2001; Miller and Kozár, 2002; Kozár, 2004; Vea and Grimaldi, 2012). Only adult females and late instar nymphs are currently identifiable because the original descriptions were based solely on the former, along with their associated nymphs. However, our understanding of adult male scale insect morphology is gradually improving, with the recognition that phylogenetic analyses based on male morphology have given us a much improved understanding of scale insect phylogeny (Hodgson and Hardy, 2013) compared with the structure of the larviform adult females. Additionally, specimens of fossil adult males of many scale insect families are commonly preserved in amber around the world (almost always without their adult female counterpart), and provide an excellent fossil record of the Coccoidea for the past 130 million years. Accurate interpretation of these fossil males, however, requires a much better understanding of the morphology of Recent ones. By reason of the rarity of adult males and the difficulty in matching them to their respective females, the adult males of only two named species of recent Ortheziidae
(Orthezia urticae (Linneaus) and Newsteadia floccosa (De Geer) have been described in detail (Koteja, 1986), although two further unidentified species assigned to the genus Orthezia have also been described (Koteja, 1986; Hodgson and Foldi, 2006). In addition, three fossil taxa, each assigned to a monotypic genus, have been described based solely on macropterous males: two preserved in Eocene Baltic amber, namely *Palaeonewsteadia huaniae* Koteja (Koteja, 1987a) and *Protorthezia aurea* Koteja (Koteja, 1987b), and one in Early Cretaceous Lebanese amber, *Cretorthezia hammanaica* Koteja & Azar (Koteja and Azar, 2008). Thus, the diversity in the morphology of male Ortheziidae is hardly known.

This study describes the adult male morphology of seven ortheziid species in five genera based on the classification of Kozár (2004): *Graminorthezia graminis* (Tinsley), *Insignorthezia insignis* (Browne), *Newsteadia americana* Morrison, *Praelongorthezia praelonga* (Douglas), *Orthezia annae* Cockerell, *Orthezia graminicola* Morrison, and *Orthezia newcomeri* Morrison. Their morphology is then compared with previous descriptions of both extant and fossil male Ortheziidae. Finally, the potential of confocal laser scanning microscopy (CLSM) is introduced here, as a tool for observing slide-mounted specimens that have been incompletely cleared. CLSM is presented as a potential and non-destructive alternative to slide remounting, for study of the cuticular details of these poorly prepared specimens.

**Materials and Methods**

This study used collection material from the Natural History Museum, London, UK and the Coccoidea collection of the United States National Museum of Natural History, housed at the U.S. Department of Agriculture, Beltsville, Maryland.
Species identification of these specimens was through each being collected with adult females in the same series (i.e., from the same host plant), except for Orthezia ?graminicola which was collected in a greenhouse with an associated female, although the latter has different collection data. Details of these collections are provided in each species account, below. All specimens had been previously slide mounted and the number of studied specimens are indicated as for instance 1/2 ad mm, where “1” refers to the number of slides and “2” the total number of adult males. These mounted specimens were in two states: (i) completely cleared preparations, where all structures were easily observable using standard compound light microscopy (these were usually more recent preparations); and (ii) older preparations, where the clearing step was skipped or incompletely done, so that many cuticular structures were obscured by internal organs, thus preventing optimal examination of the specimens under transmitted light.

Because the uncleared slide preparations could not be easily examined under conventional light microscopy, they were visualized using a Zeiss LSM 710 Confocal Laser Scanning Microscope (CLSM), at the AMNH. This method resulted in 3D reconstruction of the surface of the specimen without the need to remount the specimen thus preventing damage to the specimen.

Drawings were made using a Wild M20 compound microscope using a drawing tube or from images obtained with the CLSM. Each drawing represents the whole body, excluding the complete wings; the dorsal surface is on the left side and the ventral surface is on the right side, the convention for scale insect descriptions. Details of structures are variously enlarged around the body. Terminology follows Hodgson and Foldi (2006), except for wing venation, where Koteja’s terminology was used (see Koteja, 2008).
Abbreviations in the descriptions, definitions of which follow Hodgson and Foldi (2006), were as follows: \(fs\) for fleshy setae (thick and blunt setae lacking a sclerotized socket), \(hs\) for hair setae (hair-like setae, with a flagellate apex and a shallow setal socket), \(lp\) for loculate pores (large pores with an arrangement of 3 to 6 inner loculi), \(smp\) for simple minute pores (simple ring pores, each 1-3 \(\mu\)m across, found throughout the body), \(mcp\) for minute convex pores (each pore 3 or 4 \(\mu\)m wide, restricted to the head).

**Identification key to the Recent species of the Ortheziidae based on adult males.**

1. Hamulohalteres absent; setae on legs long and hair like.......................................................... 2
   – Hamulohalteres present; setae on legs short and spinose along ventral margin.......................................................................................................................................................... 3

2. Trochanter and femur not fused; with 3 alar setae on forewing ................................................................. *Newsteadia americana* Morrison
   – Trochanter and femur fused; with 1 alar seta on forewing ................................................................. *Newsteadia floccosa* (De Geer)

3. Compound eyes each with obviously more than 100 ommatidia; fleshy setae on body pointed apically.................................................................4
   – Compound eyes each with obviously less than 100 ommatidia; body fleshy setae thick and round......................................................*Graminorthezia graminis* (Tinsley)

4. Median ridge on sternite IX present................................................................. 5
   – Median ridge on sternite IX absent................................................................. 8
5. Antennae almost twice body length; with long fleshy setae, each twice length of other abdominal setae, present on dorsal abdominal segments………………………………………………………….. Insignorthezia insignis (Browne)

   – Antennae not longer than 1.5 X body length; fleshy setae on abdominal segments about same length as hair-like setae each twice length of other setae on dorsal abdominal segment ………………………………………………………………………………………………………..6

6. Loculate pores absent on dorsal part of epicranium; tubular duct plate on tergite VII divided into lateral groups of ducts; loculate pores on abdominal segments mainly each with 3 loculi, only occasionally with 4 loculi………………………………………………………Praelongorthezia praelonga (Douglas)

   – Loculate pores present on dorsal part of epicranium; tubular duct plate on tergite VII not divided into lateral groups of ducts, each plate complete; loculate pores each with at least 4 loculi …………………………………………………………………………………………..7

7. Body length less than 2 mm; loculate pores on abdominal sternites absent ……………………………………………………………………………………………………………………………………………………………………………………………………..Orthezia sp. (in Koteja, 1986)

   – Body length more than 2 mm, multilocular pores on abdominal sternites present ……………………………………………………………………………………………………………………………………………………………………………………………………..Orthezia sp. (in Hodgson and Foldi, 2006)

8. Each tubular duct plate on tergite VII with fewer than 10 tubular ducts; capitate setae present on antennal segments………………………………?Orthezia graminicola Morrison (but see comments in description)

   – More than 10 tubular ducts on tergite VII; capitate setae absent on antennal segments…………………………………………………………………………………………………………………………………………………………………………………………………..9
9. With less than 50 tubular ducts on tergite VII; body less than 2 mm long; setae on appendages with a mixture of short and significantly longer setae………………………………………………………….. Orthezia annae (Cockerell)

– With significantly more than 50 tubular ducts on tergite VII; body more than 2 mm long; longer setae on appendages absent………………………………………………………………………………..10

10. Dorso-midcranial ridge reaching postoccipital suture; tubular ducts on anterior margin of tergite VII surrounded by two types of peripherical setae, one almost twice as long as others and broadening at midlength; with dermal structures throughout the body except for appendages; hamulohalteres with 3 hamuli………………………………………………………….. Orthezia newcomeri Morrison

– Dorso-midcranial ridge not reaching postoccipital suture; tubular ducts on anterior margin of tergite surrounded by one type of setae; dermal structures throughout the body absent; hamulohalteres with 2 hamuli…………………………………………………………….. Orthezia urticae (L.)

Descriptions of adult males

Hemiptera Linnaeus, 1758

Sternorrhyncha Duméril, 1806

Coccoidea Fallén, 1814

Ortheziidae Amyot & Serville, 1843


Family diagnosis: Body slender, legs thin, antennae usually longer than body, antennae nine-segmented, with blent fleshy setae, with an apical bristle on the tip of apical segment; head dorsoventrally flattened with two compound eyes, and with dorsal and
ventral median ridges, loculate pores and setae usually present on head (except *Praelongorthezia*); head and thorax separated by a constricted neck; prothorax with median prosternal ridge (except *Newsteadia*); prescutum oval; scutellum subpentagonal, round anteriorly, without foramen; mesopostnotum short; basisternum with a median ridge; triangular plate absent; metathorax with a slight waist; forewings with polygonal wings discs (see Koteja, 1986); with subcostal ridge + cubital ridge + posterior flexing patch; hamulohalteres present (except for *Newsteadia*); legs slender and long, tarsus one-segmented; abdominal spiracles present; tergite VII with a group of tubular ducts; tergite VIII with a group of differentiated pores, with one loculus; penial sheath triangular, blunt.

**Family description. Head.** More or less round (sometimes wider than long). **Dorsally:** midcranial ridge well developed; dorsomedial part of epicranium sclerotized, without reticulations, becoming more sclerotized posteriorly, ending in a transverse postoccipital ridge. **Laterally:** genae absent, ocular sclerite without setae or pores, with two well developed compound eyes, number of ommatidia varies across genera, ocellus present laterally, preocular ridge short, postocular ridge usually short ventrally and longer dorsally, sometimes extending to scape (*Praelongorthezia*). **Ventrally:** midcranial ridge well developed, extending from near posterior margin of ventromedial part of epicranium dorsally almost to posterior margin of dorsomedial surface of epicranium; ventromedial surface of epicranium sclerotized but not reticulated, with ventral head setae, *lp* and *mcp*. Posterior margin of epicranium invaginated to form a shallow, transverse apophysis; ventral plate present posterior to epicranium; mouth opening medially, usually without setae on ventral plate and around mouth.
Antenna. 9-segmented, long and filiform; all segments narrow. Scape, each with short setae. Pedicel each with few $fs$ and $hs + 1$ a campaniform sensillum dorsally, somewhat removed from distal margin. Segments III–IX all long, becoming narrower towards apex: with numerous $fs$ of usually one type (except in Genus undetermined). Segment IX elongate; almost always without capitate setae but with $fs + 1$ strong terminal bristle, and sometimes short antennal bristles laterally near apex.

Thorax. Head and thorax separated by a neck constriction. Prothorax. Mostly membranous: cervical sclerites complex, anteriorly articulating with postocular ridge. Ventrally: sternum with a strongly sclerotized median ridge; transverse ridge and prosternal apophyses absent. Antemesospiracular setae fused with posterior propleural setae. Mesothorax. Dorsally: mesoprephragma broad but shallow; prescutum oval and quite large; sclerotized but without nodulations; prescutal ridge almost absent, represented by a small sclerotization anterolaterally to prescutum; margin of prescutum posteriorly delineated by a short pair of convergent, unsclerotized, prescutal sutures which do not meet medially; prescutum without prescutal setae or pores. Scutum sclerotized throughout, without nodulation, with scutal setae. Scutellum sub-pentagonal, rounded anteriorly, bounded anteriorly by scutoscutellar sutures scutellum without setae but with $lp$; posterior margin of scutellum represented by a ridge, extending laterally along posterior margin of scutum to postalare. Mesopostnotum broad but short, with a rather small membranous area anteriorly; much of mesopostnotum deeply embedded beneath metathorax as a mesoprephragma. Laterally: prealare quite long and narrow, terminating near mesepisternum; tegula sclerotized, with tegular setae. Mesepisternum nodulated near lateropleurite; subspiternal ridge long and well developed. Mesopleural
apophyses well developed, each generally with a small area of reticulation. Postalare without reticulations or setae. Postmesospiracular setae absent. *Ventrally:* basisternum well developed, with a strong median ridge, with a strong precoxal ridge; with *hs* basisternal setae distributed more or less throughout, furca large, narrow-waisted, arms rather broad and very divergent, extending almost to marginal ridge anteriorly.

Postmesospiracular setae absent. **Metathorax. Dorsally:** metapostnotum narrow but distinct across segment medially, metatergal setae and pores present. Dorsospiracular setae: *hs* and *lp* present. **Laterally:** dorsal part of metaleural ridge well developed, articulating with base of hamulohaltere. Metepisternum unsclerotized and without postmetaspiracular setae or pores; a weak precoxal ridge extends anteriormedially from posterior end of each metaleural ridge towards posterior spiracle. Antemetaspiracular setae and pores absent. Metepimeron with a sclerotized ridge running posteriorly, without setae. *Ventrally:* metasternum large and sclerotized, broader anteriorly than posteriorly, with a large subrectangular pit centrally, with strongly sclerotized lateral margins; pit opening into well-developed metafurca.

**Wings.** Forewing hyaline, without microtrichia but with polygonal discs on surface (Koteja, 1986); subcostal ridge usually extending on anterior margin to about ¾ wing length, cubital ridge originating at one fifth from wing base; when other veins present, only posterior flexing patch apparent; alar fold present but very narrow when hamulohaltere present. Hamulohalteres long and narrow when present (absent in *Newsteadia*), with apical hamuli on anterior margin at distal end of sclerotized ridge.

**Legs.** Mesothoracic shortest, others subequal in length. Long setae on coxa and trochanter not differentiated. Fleshy setae (*fs*) not differentiated from *hs*. Each trochanter
with campaniform sensillae, more or less in a straight line; separation of trochanter and femur distinct, almost at right angles to leg margin, probably without an articulation.

Tibia with setae, becoming spur-like on distal half to two-thirds, particularly on ventral side. Tibia with setae, becoming spur-like on distal half to two-thirds, particularly on ventral side. Tarsus with spur-like setae; tarsal spurs not differentiated; tarsal campaniform sensilla present and convex; tarsal digitules very short and spinose, usually not differentiated. Claws fairly long and narrow, much longer than width of tarsus; claw digitules spinose or setose both shorter than claw, denticle almost always present.

**Abdomen.** **Segments I–VII:** tergites lightly sclerotized; sternites also lightly sclerotized but with distinct, sclerotized, intersegmental ridges. Presence of loculate pores and distribution varies across genera. Tubular ducts present in a band across tergite VII (or on two separate plates in *Praelongorthezia*), inner surface of each duct with shallow spiral ridges. Abdominal spiracles at least present on anterodorsal part of pleurites I–VIII but more or less easily detectable across species. **Segment VIII:** tergite unsclerotized; sternite lightly sclerotized but with a strongly sclerotized crescentic ridge along anterior and lateral margins, fusing with sclerotization of penial sheath posteriorly; tergite with *hs* dorsal abdominal setae, plus locular pores (these absent in *Newsteadia* only), structurally different from *lp* on other abdominal segments (by being slightly smaller, and having an external ring divided in many small compartments, and deprived of inner large loculi; see Discussion section) and many *smp*; margin rounded, pleural *hs* present; sternite with ventral abdominal setae but no pores, sometimes with a median ridge.

**Genital segment.** Segment X represented by area immediately around anus on dorsal surface but also fused with segment IX dorsally, represented by a sclerotized area in anal region; *hs* present on tergite IX; anus large with a lightly sclerotized area along anterior
margin; sternite IX represented by a large sclerotized sternal plate (present of a median
ridge and/or setae varies across genera). Penial sheath broad, triangular and blunt;
ventrally and laterally with a group of short, apically rounded setae on each side of
anterior end of penial sheath; posteriorly, minute setae absent on either surface near apex.
Aedeagus parallel-sided anteriorly but becoming pointed posteriorly in dorsal view (apex
broader in *Newsteadia*), extending to near apex of penial sheath. Penial sheath with a
small group of sensilla near apex.

**Graminorthezia Kozár**


**Generic diagnosis:** Compound eyes with about 60 large ommatidia; antennal segments
relatively shorter (1.17 times body length as opposed to 1.3 to 2 for other genera), scape
almost square-shaped; *hs* on body and appendages thicker, with a blunt apex; head
midcranial ridge with dorsal arm thinner and fading posteriorly; ventral plate rectangular;
prothoracic pronotal setae anteriorly on shoulder dorsally; abdomen with *lp* at least on
dorsopleurites; abdominal spiracles at least present on pleurites II-VI.

**Comments:** *Graminorthezia* currently comprises 11 described species. The present
generic diagnosis only accounts for *Graminorthezia graminis*. The genus was defined on
the basis of adult female morphology and distinguished from other genera by “no more
than 7 abdominal spiracles”.

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Graminorthezia graminis (Tinsley)

(Figures 3.1; 3.2; 3.3A)

Orthezia graminis Tinsley, 1898:13-14.

Material examined: USA, New Mexico, Dona Ana, on “grass”, 26. ix. 1897, Townsend coll. (USNM): 1/ad male (in good condition but uncleared, description of specimens based on confocal microscope images and thus some pores and setae not observable and mentioned as such).

Diagnosis: As for genus.

Description: Mounted material. Body length 1.9 mm. Antenna nearly 1.17× body length, most segments approximately subequal in length, with numerous fs present on antenna, randomly distributed. Hair setae, lp, smp and mcp almost all (but described when otherwise) not observable on available specimens.

Head. Broad, wider than long (280 μm wide, 225 μm long). Dorsally: midcranial ridge as for family. Dorsomedial part of epicranium sclerotized as for family; setae and pores not visible. Laterally: Compound eye about 100 μm long, with about 60 ommatidia. Ocellus 25–30 μm wide. Ventrally: midcranial ridge as for family; ventral setae and pores not visible. Ventral plate rectangular, mouth opening and preoral ridge as for family.

Antenna. Total length 2.28 mm (ratio of body length to antennal length 1:1.17). Scape almost square shaped: 78–92 μm long, 73–82 μm wide, each with probably 4 or 5 short setae. Pedicel: length 73–82 μm, width 52–60 μm; each with at least 3 or 4 fs + a campaniform sensillum dorsally, somewhat removed from distal margin. Segments III–IX all long, becoming narrower towards apex, proximal segments about 40–50 μm wide,
Figure 3.1. Dorsal surface of *Graminorthezia graminis* (Tinsley). **A.** Compound light microscope, **B.** Confocal microscope. Scale bar: 500 µm.
Figure 3.2. Illustration of *Graminorthezia graminis* (Tinsley). Adult male. A. Thick and blunt setae on head and body, B. Antennal apical seta, C. Leg seta, D. Tibiotarsal connection, E. Claw.
Figure 3.3 Confocal microscope images of the male genital segments of four genera in the Ortheziidae. A. *Graminorthezia graminis* (Tinsley), B. *Insignorthezia insignis* (Browne), C. *Orthezia newcomers* Morrison, D. *Praelongorthezia praelonga* (Douglas). Scale: 100 µm.

**Thorax. Prothorax.** Dorsally: Post-tergites and pronotum not detected, possibly absent. Pronotal setae: 2 hs anterior propleural setae anteriorly on shoulder; no other setae observed. Ventrally: cervical sclerites complex: anteriorly articulating with postocular ridge. Sternum with a strongly sclerotized median ridge; transverse ridge and prosternal apophyses absent; prosternal setae not detected but probably present. Anteprosternal setae probably absent. Antemesospiracular setal group probably fused with group of posterior propleural setae.

**Mesothorax.** Dorsally: prescutum 90 µm long, 135 µm wide; sclerotized but without nodulations; mesoprephragma not observable but probably shallow; prescutal ridge almost absent, represented by a small sclerization anterolaterally to prescutum; margin of prescutum posteriorly delineated by a short pair of convergent, unsclerotized, prescutal sutures which do not meet medially; prescutal ridge continuous with scutum posteriorly; prescutum without prescutal setae or pores; distance between prescutum and scutellum medially 80 µm; scutal setae with 4 or 5 hs medially posterior to prescutum; hs near lateral margins not observed. Scutellum rounded anteriorly, 169 µm wide, 125 µm long; bounded anteriorly by scutoscutellar sutures; scutellum without setae but with 2 or 3 lp; posterior margin of scutellum represented by a ridge, extending laterally along posterior
margin of scutum to postalar. Mesopostnotum as for family, postnotal apophyses probably well developed but not observable. Laterally: prealar quite long and narrow, terminating near mesepisternum; tegula sclerotized, with 3 tegular setae. Postalare without setae. Mesothoracic spiracle with peritreme almost round, width 40 µm.

Ventrally: basisternum as for family with a median ridge, 400 µm wide, 182 µm long, with 8–10 hs basisternal setae, distributed more or less throughout; lateropleurite as for family; furca not observable. Postmesospiracular setae not detected, probably absent.

Metathorax. Dorsally: metapostnotum as for family; metatergal setae and pores not observed. Dorsospiracular setae: at least 2 hs + 3 lp present. Laterally: dorsal part of metapleural ridge well developed, articulating with base of hamulohaltere. Antemetaspiracular setae not detected. Ventrally: metasternum large and sclerotized, broader anteriorly than posteriorly, with a large subrectangular pit centrally, with strongly sclerotized lateral margins; pit opening into well-developed metafurca; setae and pores not observable. Metathoracic spiracle with peritreme almost round, width 35 µm.

Wings. Forewing hyaline, 1940–2040 µm long, about 705–765 µm wide (ratio of length to width 1: 0.37; ratio of body length to wing length 1: 1); with subcostal ridge extending on anterior margin to about \( \frac{3}{4} \) wing length, cubital ridge originating in basal fifth of wing; only posterior flexing patch apparent; alar fold present but very narrow; without alar setae; circular sensoria not observable on available specimens but most probably present along posterior margin of subcostal ridge Hamulohalteres long and narrow, without microtrichia, each about 212–247 µm long, 35–40 µm wide, with 2 apical hamuli placed on anterior margin at distal end of sclerotized ridge; each hamulus about 50 µm long.
**Legs.** Relative length of legs as for family. Fleshy setae not differentiated from hair-like setae. Coxae: I 138–144; II 129–147; III 142–147 µm long; coxa III with at least 3 setae; long setae on coxae not differentiated. Trochanter + femur: I 400–518; II 408–450; III 490 µm long; trochanter III with 3 or 4 setae; each trochanter with 3 campaniform sensilla, more or less in a straight line; separation of trochanter and femur distinct, almost at right angles to leg margin, probably without an articulation; long trochanter seta absent; femur III with about 45 setae. Tibia: I 695; II 560–630; III 670–675 µm; tibia III with about 70 setae, these becoming spur-like on distal half to two-thirds, particular on ventral side; spurs on ventral surface of distal end each 14–27 µm long. Tarsi: I 225; II 230–240; III 225–235 µm long (ratio of lengths of tibia III to tarsus III 1: 0.34); tarsus III with about 35 setae, mainly spur-like; tarsal spurs not differentiated from setae; tarsal campaniform sensilla present and convex; tarsal digitules very short and spinose. Claws as for family, much longer than width of tarsus (each tarsus about 25 µm long), III 50 µm long; each with a minute denticile; claw digitules both shorter than claw and spinose.

**Abdomen.** *Segments I–VII:* tergites lightly sclerotized; sternites also lightly sclerotized but with distinct, sclerotized, intersegmental ridges. Loculate pores only detectable on dorsopleurites, loculate pores on tergites and sternites not observable. Tubular ducts present in a band across tergite VII, each duct 6–10 µm wide, 15 µm deep, inner surface of each duct with shallow spiral ridges. Dorsal abdominal setae and pores (totals): segments I–V 4 hs; VI 4 hs; VII about 20 hs and between 24 and 35 tubular ducts, in a band about 3 ducts wide. Pleural setae: dorso- and ventropleural setae combined on each side: I–VII 3 or 4 hs + at least 5 lp. Ventral abdominal setae and pores not observable.
Abdominal spiracles present on anterodorsal part of pleurites I–VI, and possibly present on pleurite VII; each peritreme about 13 μm wide. *Segment VIII:* tergite unsclerotized; sternite lightly sclerotized but with a strongly sclerotized crescentic ridge along anterior and lateral margins, fusing with sclerotization of penial sheath posteriorly; tergite with 1 pair *hs* dorsal abdominal setae plus about 60 Small locular pores and many *smp*; sternite with setae but number uncertain; pores believed to be absent; margin rounded, with 2 or 3 *hs* pleural setae. Abdominal spiracles not detected but probably present.

**Genital segment.** Segment X as for family; with 2 or 3 *hs* dorsally; anus 40 μm wide, with a lightly sclerotized area along anterior margin; ventrally, segment IX represented by a large sclerotized sternal plate, with a median ridge; with at least 3 or 4 setae on each side. Penial sheath broad, width similar to posterior margin of abdominal segment VIII, triangular and blunt; length without segment IX 260 μm, with segment IX 365 μm; greatest width 170 μm; ventrally and laterally with a group of about 15 short, apically rounded setae on each side of anterior end of penial sheath; posteriorly, minute setae absent on either surface near apex. Aedeagus parallel-sided anteriorly but becoming pointed posteriorly in dorsal view, extending to near apex of penial sheath; length about 225 μm. Penial sheath with a small group of sensilla on near apex.

**Comments:** Two uncleared specimens were available for which confocal images were obtained. Most of the structures were observable apart from some pores and setae on the thorax and the abdominal sternites. Some setae could be identified by their basal sockets, which are visible with the confocal images. However, locular pores were mostly not identifiable and so mentioned as not observable in the description; minute simple pores could not be detected with confocal images. Despite these missing details, it is clear that
**Graminorthezia** is distinguishable from *Orthezia* based on male morphology. The specific characters are the thick and stout setae, the shorter appendages and the compound eyes with larger and fewer ommatidia (i.e. about 60).

**Insignorthezia Kozár**


**Generic diagnosis:** Antennae unusually long, almost twice body length; dorsal abdominal setae long; *lp* triangle-shaped with 3 loculi, although sometimes with 4 loculi; head broad, almost wider than long; compound eyes with 150 ommatidia; midcranial ridge with dorsal arm strong and fading posteriorly, ventral arm extending to midlength of head, fusing with preoral ridge and bifurcated posteriorly; prothorax with dorsally, mediolateral post-tergite, as lightly slerotized oval area, median pronotal setae present; with a group of posterior propleural setae and pores just anterior to each prealare, extending ventrally and joining antemesospiracular setae, mesothorax with sctellum bearing *lp* and *msp*, but no setae; abdomen with sternite devoid of locular pores, but present on tergite partly and pleurites II-IV. Abdominal spiracles present at least on anterodorsal part of pleurites III–VII; sternite VIII without a median ridge.

**Comments:** *Insignorthezia* comprises 10 described species. The present generic diagnosis only accounts for *Insignorthezia insignis*. *Insignorthezia* was defined based on adult female morphology and distinguished from *Graminorthezia, Praelongorthezia* and *Orthezia* (all belonging to the Ortheziini) by the “absence of bands or rows of wax plates within the ovisac band” (Kozár, 2004: 271). The adult male of *Insignorthezia insignis* is unique in having extremely long appendages, particularly the antennae, which are almost twice as long as body length compared to other genera, as well as a pair of very long
setae on each tergite. Loculate pores of 3 or 4 loculi are present on the pleurites and overlapping on tergites but absent on sternites. Sternite VIII does not have a median ridge.

_Insignorthezia insignis_ (Browne)

(Figures 3.3B; 3.4)

_Orthezia insignis_ Browne, 1887: 169-172.

**Material examined:** CEYLON (SRI LANKA), Paredeniya, xi. 1940, E.E. Green coll., 1/5ad male, deposited at BNHM.

**Diagnosis:** As for genus.

**Description: Mounted material.** Moderately large, total-body length 1.66–1.76 mm. Antennae exceptionally long, nearly 2 times total-body length, most segments approximately subequal in length. Body with few setae, all _hs_, each with a broad, flattish socket although some setae on legs and abdominal sternites rather long and _fs_-like but here considered to be larger _hs_; _lp_ each 7–8 µm wide, with mostly 3 loculi, occasionally 4, present on both dorsal surface.

**Head.** Shape as for family, 285 µm wide and 300 µm long. _Dorsally:_ midcranial ridge well developed and dorsomedial part of epicranium sclerotized as for family, with (on each side) about 5 _hs_ of rather variable length (20–50 µm), all flagellate, plus 2 _lp_ and 1 or 2 _mcp_. _Laterally:_ Compound eye about 155 µm long, with about 160 ommatidia. Ocellus 30–40 µm wide. _Ventrally:_ midcranial ridge well developed and ventromedial part of epicranium as for family. Ventral head setae: with (on each side) 8–12 _hs_ plus 1–4 _lp_ + 3 or 4 _mcp_.

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Figure 3.4. Illustration of *Insignorthezia insignis* (Browne). Adult male. A. Antennal apical seta, B. Claw, C1. Abdominal pore with 4 loculi, C2. Abdominal loculate pore with 3 loculi, D. Tubular duct with peripheral seta, E. Small locular pore, F. Penial sheath.
**Antenna:** Shape as for family, 3.23 mm long (ratio of total-body length to antennal length 1: 1.9). Scape: 94–117 µm long, 63–80 µm wide, each with 6 or 7 short hs + 2 or 3 minute pores ventrally and 4 hs dorsally. Pedicel: 65–85 µm long, 49–57 µm wide; each with 3 fs, 5 or 6 hs, 3 minute pores ventrally + a campaniform sensillum dorsally. Segments III–IX all rather long, becoming slightly narrower towards the apex, those proximally about 36–43 µm wide, while apical segment only 15–24 µm wide: fs short, those on segment III 28–38 µm long, those on apical segment 25–30 µm long; lengths of segments (µm): III 369–405; IV 433–479; V 423–509; VI 381–520; VII 400–494 and VIII 400–600; approximate number of setae per segment: III–VIII; about 45–70 fs +10–15 hs; no bristle-like setae detected on these segments. Segment IX elongate: 346–412 µm long; without capitate setae but with about 80 fs + 1 strong terminal bristle, about 35 µm long + 1 antennal bristle laterally near apex; coeloconic sensilla not detected.

**Thorax. Prothorax:** Dorsally: pronotum not observable. Post-tergites each a small, lightly sclerotized, oval area situated mediolaterally. Pronotal setae: median pronotal setae: 1 hs plus 2 or 3 lp + 2 or 3 smp; propleural setae not detected; also with a group of posterior propleural setae and pores just anterior to each prealare, extending ventrally and joining antemesospiracular setae: 1 hs, 5–6 lp + 3–5 smp. Ventrally: cervical sclerites complex: anteriorly articulating with postocular ridge. Basisternum as for family; with 1 hs prosternal setae + 1 lp on each side. **Mesothorax. Dorsally:** prescutum, 97 µm long, 134 µm wide; ridges as for family. Distance between prescutum and scutellum medially 97–117 µm; with about 2 hs scutal setae: + 15 minute pores medially posterior to prescutum. Scutellum 170–181 µm wide, 109–112 µm long, with 2 lp + 3 smp; ridges and sutures as genus. Mesopostnotum as family. **Laterally:** prealare as for family, tegula
with 2 or 3 setae. Mesothoracic spiracle: peritreme almost round, width about 30 μm. *Ventrally:* basisternum as for family, 390 μm wide, 180 μm long; with about 10 hs basisternal setae; lateropleurite as for family; furca as for family. Postmesospiracular setae absent. **Metathorax.** Dorsally: metapostnotum ridge with 2 metatergal setae. Dorsospiracular setae: 1 hs plus 2 lp. Laterally: Main structures as for family. Antemetaspiracular setae probably absent. Metathoracic spiracle: peritreme almost round, width 35 μm. *Ventrally:* metasternum as genus; sclerotized area with 3–5 hs + 1 lp + some smp on each side; occasionally with 1 hs anterior metasternal seta and 0 or 1 hs posterior metasternal setae.

**Wings.** Forewing length and width unknown because of wings damaged due to slide preparation, main structures as for family. Hamulohalteres as for family.

**Legs.** Coxae: I: 126–160; II: 129–148; III: 136–146 μm long; coxa III with about 4 setae; long setae on coxae not differentiated. Trochanter + femur: I: 603–686; II: 527–597; III: 603–673 μm long; trochanter III with about 5 setae; each trochanter with 4 campaniform sensilla arranged in a line on each side; separation of trochanter and femur as for family; femur III with about 40 setae + 10 smp. Tibia: I: 882–804; II: 776–805; III: 801–918 μm; tibia III with a total of about 115 setae, these becoming spur-like on distal half to two-thirds, particular on ventral side + 5 smp; spurs on ventral surface of distal end of tibia similar to those more anteriorly; each distal spur 26–30 μm long. Tarsi: I 187–200; II 184–212; III 194–212 μm long (ratio of length of tibia III to length of tarsus III 1: 0.44); tarsus III with about 30 setae, mainly spur-like; tarsal spurs not differentiated; tarsal campaniform sensilla present and convex; tarsal digitules very short and setose. Claws fairly long and thin, much longer than width of tarsus (each tarsus about 25 μm wide),
held at a distinct angle to tarsus, each with a small denticle; length: III 60 µm; claw
digitules both short and setose.

**Abdomen.** *Segments I–VII:* structures as for genus. Tubular ducts present in a band
across tergite VII, each duct 8 µm wide, 20 µm deep, with a slightly spirally-ridged inner
surface. Dorsal abdominal setae and pores (totals): segments I–V: 4 extremely long *hs*
(80–100 µm); VI: 4 extremely long *hs + lp*, group fusing with pleurites; VII: about 20 *hs*
and 20–25 tubular ducts. Pleural setae: dorso- and ventropleural setae combined on each
side: I–VII: 3 or 4 *hs + 12–20 lp + 15–25 smp*, most setae about 50–60 µm long. Ventral
abdominal setae fleshy and shorter than dorsal abdominal setae, each 35–40 µm long
(totals): I 8 *fs*, 0 lp; II: 8 or 9 setae, 0 lp; III–VI 10–12 *fs*, 0 lp; VII 6–8 *fs*, 0 lp.
Abdominal spiracles distribution as for genus, each peritreme about 10 µm wide.

*Segment VIII:* structures as genus, tergite with 1 or 2 pairs of *hs* dorsal abdominal setae,
about 40 locular pores, different from other *lp* on abdomen, and many *smp*; sternite with
about 10 ventral abdominal setae but no pores; margin rounded, with 2–4 *hs* pleural setae,
3–4 *lp + 2–4 smp.*

**Genital segment.** Segment X and IX as for family; anus large (32 µm wide), with a
lightly sclerotized area along anterior margin and with 1 or 2 *hs* on tergite IX; sternite IX
with 3–4 setae. Penial sheath as broad as posterior margin of abdominal segment VIII,
short, triangular and blunt; length without segment IX 190 µm, with segment IX 243 µm;
greatest width 140 µm; ventrally and laterally with a group of 20 *hs* on each side of
anterior end of penial sheath; posteriorly, nearer apex, without minute setae on either
surface. Aedeagus shape as for family; length about 170–190 µm.
**Newsteadia Green**


**Generic diagnosis:** *Newsteadia* differs from the other genera with the following characters: head with dorsal midcranial ridge strong arm but fading posteriorly, ventral midcranial ridge with arm strong and bifurcating posteriorly, compound eyes with 30-50 ommatidia (reduced compared to >60 and usually >100 for other genera); prothorax: sternum with a triangular sclerotized area with well-sclerotized margins; mesothorax: scutellum without setae or pores but with *smp*; scutum with median area short, without *hs* near lateral margins; metathorax with metatergal setae and pores present, but without *smp*; wing-shape round with reduced venation compared to other Ortheziidae (subcostal and cubital ridges only present); alar lobe or fold absent; hamulohalteres absent (present in *Orthezia, Praelongorthezia, Insignorthezia, Graminorthezia*); legs longer *hs*; abdomen with tergite VIII without any small locular pores, sternite VIII without pores or setae; apex of aedeagus of unique shape, widening at tip, probable absence of sternite IX.

**Newsteadia americana Morrison**

(Figure 3.5)

*Newsteadia americana* Morrison, 1925: 147-150.

**Diagnosis:** *Newsteadia americana* differs from *N. floccosa* because of the absent lateral branch of dorsal midcranial ridge (vs. present), same ridge fading before postoccipital ridge (vs. bifurcating posteriorly); trochanter and femur unfused (fused on *N. floccosa*), number of tubular ducts smaller than *N. floccosa*.

**Description:** *Mounted material.* Total body length 1.63 mm. Antennae nearly 1.3 times total body length, most segments with many short setae; body with few setae, all *hs*, each with a broad, flattish socket; some setae on legs and abdomen rather long but here considered to be larger *hs, fs* therefore restricted to antennae and legs; lp absent, but smp, each 2–3 µm wide, present sparsely throughout body.

**Head.** 260 µm wide and 225–250 µm long. *Dorsally:* midcranial ridge and dorsomedial part of epicranium as for genus; with (on each side) 2 or 3 *hs*, (each mainly about 55 µm long), all flagellate, plus 1 or 2 *mcp* near midcranial ridge. *Laterally:* Compound eyes each about 95 µm long, each with about 45–50 ommatidia; ocellus 25 µm wide; Preocular ridge as for genus. *Ventrally:* midcranial ridge extending and ventromedial part of epicranium as for genus; with 7–10 longish *hs* ventral midcranial ridge setae (each about 50 µm long) + 4–8 *mcp* on either side of ventral midcranial ridge. Other structures as for genus.

**Antenna:** total length 2.08 mm (ratio of total-body length to antennal length 1: 1.28). Scape: 124 µm long, 57–60 µm wide, each with 10–12 rather long *hs* distally (each about 40 µm long) plus a rather spinose seta near base dorsally, without pores. Pedicel: length 82–84 µm, width 50 µm; each with 5 or 6 *hs*, 3 coeloconic sensilla ventrally + a campaniform sensilla dorsally, somewhat removed from distal margin. Segments III–X all rather long, becoming slightly narrower towards apex, those proximally about 26 µm
wide, while apical segment only about 20 µm wide; *fs* quite long, each about 43 µm long on basal segments but shorter on apical segment (some only 30 µm long); *hs* short, mostly 15–18 µm long; lengths of segments (µm): III 340–365; IV 335–360; V 320–335; VI 281–290; VII 240; VIII 185–188, and IX 185–195; approximate number of setae per segment: III–VIII each with about 16–18 *fs* + 2–6 *hs*; no bristle-like setae detected on these segments. Segment IX elongate, without capitate setae but with about 17 *fs*, 2 *hs* medially + 1 strong terminal bristle, about 30 µm long, and 1 antennal bristle laterally near apex, 45–50 µm long; coeloconic sensilla not detected.

**Thorax. Prothorax.** Structures hard to see as partially covered by prescutum. *Dorsally:* Post-tergites and pronotum not detected, possibly absent. No setae or small convex pores detected dorsally. *Laterally:* proepisternum + cervical sclerites complex but structure unclear on single specimen: anteriorly probably articulating with postocular ridge; structure probably similar to that on *N. floccosa* (see Koteja, 1986); pleural apophysis quite large. With 1 *hs* antemesospiracular seta on each side. *Ventrally:* sternum and prosternal apophyses as for genus; number of prosternal setae uncertain but with 1 *hs* anteprosternal seta. **Mesothorax.** *Dorsally:* mesoprephragma broad but shallow; prescutum, length uncertain but 207 µm wide; prescutal ridge almost absent, represented by a small sclerotization at anterior end; posteriorly, margin of prescutum delineated by a thin suture; prescutum without prescutal setae or pores. Prealare quite long, perhaps rather broad and well sclerotized, terminating near mesepisternum Scutum as for family, median area short, about 20 µm long; with 2 or 3 pairs of *hs* scutal setae + 0–2 minute pores on each side medially posterior to prescutum; without hs near lateral margins. Scutellum 145 µm wide and 128 µm long; bounded anteriorly by heavily sclerotized
scutoscutellar suture; scutellum without setae but with 0 or 1 pair \textit{smp}; posterior margin of scutellum marked by a thick ridge, which extends posterolaterally as posterior notal wing process to postalare. Mesopostnotum broad but short, with a rather small membranous area anteriorly; much of mesopostnotum deeply embedded beneath metathorax as a mesostophragma; postnotal apophyses well developed. \textit{Laterally}: Tegula sclerotized, with 2 tegular setae but probably no \textit{smp}. Mesepisternum not reticulated near lateropleurite; subepisternal ridge long and well developed. Mesopleural apophysis unclear. Postalare without reticulations; postalare setae absent. Mesothoracic spiracle: \textit{peritreme} almost round, width 35 \textmu m. Postmesospiracular setae absent. \textit{Ventrally}: basisternum as for family, 375 \textmu m wide, 170 \textmu m long; with 9 or 10 \textit{hs} basisternal setae + 0 or 1 \textit{smp} on each side; furca large, narrow-waisted, arms rather broad and very divergent, extending almost to marginal ridge anteriorly. \textbf{Metathorax}. \textit{Dorsally}: metatergal setae: 4 present medially and 2 more laterally on each side, but without \textit{smp}; metapostnotum present medially, small. \textit{Laterally}: dorsospiracular setae absent and without \textit{smp}. Dorsal part of metapleural ridge well developed but without hamulohalteres or suspensorial sclerites. Posterior part of metapleural ridge well developed; without "reticulations" along dorsal margin; metepisternum mildly sclerotized, without postmetaspiracular setae but with a few \textit{smp}. Metepimeron represented by a sclerotized ridge running posteriorly, without setae. Antemetaspiracular setae probably absent. Metathoracic spiracle: \textit{peritreme} almost round, width about 30 \textmu m. \textit{Ventrally}: metaprecoxal ridge strong, extending ventrally and appearing to fuse with a ridge along posterior margin of metasternum. Metasternum large and sclerotized, broader anteriorly than posteriorly, with a large subrectangular pit centrally, with strongly
sclerotized lateral margins which fuse with metaprecoxal ridges; pit opens into a pair of metafurca; sclerotized area with a line of 6 long hs posterior metasternal setae on each side; apparently without anterior metasternal setae or pores.

**Wings:** General shape as for genus, 2.0 mm long, about 875 µm wide (ratio of length to width 1: 0.44; ratio of total-body length to wing length 1: 1.23), each wing with 3 alar setae plus a line of about 8–13 circular sensoria. Other structures as for genus.

**Legs:** mesothoracic legs shortest, others subequal in length. Fleshy setae few, short, with a blunt apex, easily separable from hair-like setae, without smp. Coxae: I 127; II 117–120; III 114–120 µm long; coxa III with about 13 hs; anterior surface of each coxa with plate-like microridges with microspines. Trochanter + femur: I 485–493; II 405–408; III 450–460 µm long; trochanter III with 2 long setae (one about 25 and other about 65 µm long) + 1 fs (about 12 µm long); each trochanter with 3 oval sensoria on each side, arranged in a line, plus another more proximally; with a ridge between trochanter and femur (almost at right angles to margin) but probably with no articulation; femur III with about 45 long hs. Tibia: I 545–555; II 525–530; III 600–605 µm; tibia III with many long hs (longest about 75 µm), these becoming spur-like on distal half to one-third, particular on ventral surface (each spur 20–25 µm long) plus 4 or 5 fs, each about 20 µm long.

Tarsi: I 205–220; II 215; III 225–240 µm long (ratio of length of tibia III to tarsus III 1: 0.39); tarsus III with many setae, mainly spur-like, but with 3 or 4 fs; claws length (III) 48–56 µm, with a hint of a small denticle.

**Abdomen.** *Segments I–VII:* tergites as for genus. Tubular pores: 13 present in a narrow band across tergite VII, each about 16–18 µm long, 7 µm widest, with a more heavily sclerotized inner end. Dorsal setae and pores (totals): segments I and II: 8–10 hs + 0–2
III–VI: 8–12 hs + 12–16 smp; VII: about 36 hs, 13 tubular ducts + 0 smp; dorsal setae each about 33–35 µm long. Laterally: caudal extension of segment VII absent.

Pleural setae: dorso- and ventropleural setae combined on each side: I–VII 3–6 hs + 2–5 smp; some setae rather long, up about 55 µm. Abdominal spiracles as for genus, each peritreme extremely small (perhaps 3 µm wide), opening into a narrow, inner ductule about 13 µm long, before expanding into a wider trachea. Ventrally: sternites as for genus. Ventral setae similar to dorsal abdominal setae but longer, each about 50 µm long; (totals): I and II: 4 setae + 0 smp; III and IV: 16 setae + 10–12 smp; V and VI: 8–10 setae + 12–14 smp; VII: 4 setae on each side + 2 smp. Segment VIII: with 3 or 4 long hs dorsal abdominal setae (each 50–60 µm long).

**Genital segment.** Anus about 32 µm wide. Penial sheath 330 µm with segment VIII and 200 µm without; greatest width 215 µm; with a group of 8 or 9 short, rather blunt fs on either side of basal rod, each about 10 µm long; plus a further group of 3 or 4 fs on each margin anteriorly, each about 13 µm long; and a line of 6 or 7 fs along each posterior margin, each about 7 µm long; each side of penial sheath apex with a group of about 10 sensoria. Aedeagus about 200 µm long; articulating anteriorly with a short, quite heavily sclerotized basal rod about 40 µm long.

**Orthezia Bosc d’Antic**


**Generic diagnosis:** Head broad, wider than long, with setae and pores present on both sides; compound eyes with between 100 and 150 ommatidia. Antennal apical segment with a terminal bristle and no subapical bristle. Mesothoracic scutal setae and pores
present, anteprosternal sete absent; scutellum with loculate pores and \textit{smp}, tegula with setae and \textit{smp}; Wings with subcostal ridge often extending to less than $\frac{3}{4}$ wing length, cubital ridge starting from $\frac{1}{8}$ wing base, hamulohalteres with 2 or 3 hamuli. Legs with \textit{hs} mostly on femur and \textit{fs} on tibia and tarsus; claws with denticles and setose digitules. Abdomen with tergite VII with a single plate bearing numerous tubular ducts, surrounded by fleshy setae of variable length Sternite IX without a median ridge but with a few setae.

\textit{Orthezia annae Cockerell}

(Figures 3.6; 3.7)


\textbf{Material examined:} U.S.A., New Mexico, on "Atriplex", 11. i. 1897, Townsend coll.: 1/2 adult males (in good condition but uncleared, description of specimens based on confocal microscope images and thus some pores and setae not observable and mentioned as such).

\textbf{Diagnosis:} \textit{Orthezia annae} differs from other \textit{Orthezia} sp. in having longer antennal setae, particularly some on legs, similar to those on antennal setae, and fewer tubular ducts than on other \textit{Orthezia} spp.

\textbf{Description: Mounted material:} Body large, total-body length 1.5–1.65 mm. Antennae 1.3 times total-body length, most segments subequal in length, with numerous short setae; fleshy setae present on antennae. Body with few setae, all \textit{hs}, each with a broad, flattish socket although some setae on legs and abdominal sternites rather long and \textit{fs}-like but here considered to be larger \textit{hs}. 
Figure 3.6. Ventral surface of *Orthezia annae* Cockerell. A. Light compound microscope, B. Confocal microscope. Scale bar: 500 µm.
Figure 3.7. Illustration of *Orthezia annae* Cockerell, adult male. A. Antennal apical segment, B. Tibiotarsal connection, C. Claw. NB: Because the specimens were uncleared, this figure only illustrates structures visible under both the light microscope and in the confocal images.
**Head.** Shape as for family, 300 µm wide, 250 µm long. *Dorsally:* midcranial ridge and dorsomedial part of epicranium as for family; with at least 4 or 5 *hs; lp* and *smp* not observable. *Laterally:* Compound eye about 115 µm long, with about 100 ommatidia; ocellus 23–30 µm wide. *Ventrally:* midcranial ridge and ventromedial part of epicranium as for family; ventral head setae present. Other head structures as for family.

**Antenna:** Segmentation as family, total length 2.06 mm (ratio of total-body length to antennal length 1:1.3). Scape: 70–88 µm long, 75–79 µm wide, each with at least 5 short hair-like setae ventrally and 1 *hs* dorsally. Pedicel: length 68–70 µm, width 57–61 µm; each with 2 *fs*, 6 or 7 *hs* + a campaniform sensillum dorsally, latter somewhat removed from distal margin. Segments III–IX becoming narrower towards apex, those proximally about 40 µm wide, while apical segment only 22–26 µm wide: *fs* long, those on segment III 60–65 µm long, those on apical segment 45–50 µm long; lengths of segments (µm): III 248–257; IV 312–465; V 260–350; VI 291–352; VII 223–329 and VIII 179-256; approximate number of setae per segment: III–VIII with about 35–50 *fs*. Segment IX shortest: length 179–233 µm; with about 15 *fs* + 1 strong terminal bristle, about 45–50 µm long and 2 short antennal bristles laterally near apex.

**Thorax. Prothorax.** *Dorsally:* pronotum and post-tergites not observable. All pronotal setae and pores not observable. *Ventrally:* Sternum with a sclerotized median ridge with at least 1 *hs* prosternal seta on each side, transverse ridge and apophysis as for family. Anteprosternal setae and pores not observable. Antemesospiracular setae and posterior propleural setae not observed but probably present. **Mesothorax.** *Dorsally:* prescutum 95 µm long, 170 µm wide; prescutal ridges and sutures as for family; prescutum without prescutal setae or pores. Scutum as for family; distance between prescutum and scutellum...
medially 50 µm; scutal setae: with at least 3 hs medially posterior to prescutum.

Scutellum 170 µm wide, 120 µm long; margins and sutures as in genus; without setae or pores, or at least not observable. Mesopostnotum and posnotal apophysis as family. 

*Laterally:* prealare as for family; tegula with 3 setae. Mesopleural apophyses well developed. Postalare without postalare setae. Mesothoracic spiracle most probably present but not observable. *Ventrally:* basisternum as for family, 310 µm wide, 210 µm long; with 10–12 hs, distributed more or less throughout; lateropleurite as for family; furca not observable. Postmesospiracular setae not observable. **Metathorax. Dorsally:** metatergal setae and dorsospiracular setae not observable. *Laterally:* dorsal part of metapleural ridge well developed, articulating with hamulohaltere. Metepimeron with a sclerotized ridge running posteriorly, without setae. Antemetaspiracular setae probably absent. Metathoracic spiracle most probably present but peritreme not observable.

*Ventrally:* metasternum large and sclerotized, broader anteriorly than posteriorly, with a large subrectangular pit centrally, with strongly sclerotized lateral margins; setae and pores not observable.

**Wings.** Forewing 1.9–2.0 µm long, about 638–796 µm wide (ratio of length to width 1:0.37; ratio of total-body length to wing length 1: 1.23), base of the wing especially narrow; with subcostal ridge extending to less than ¾ of wing length, cubital ridge starting 1/8 of wing base; without alar setae, circular sensoria along posterior margin of subcostal ridge detected but number difficult to define, sensoria extending to ¾ of wing length to where subcotal ridge disappears. Hamulohaltere 225 µm long, 30 µm wide; with 2 apical hamuli; each 55 µm long.

**Legs.** Leg setae 13–20 µm long but with additional, significantly longer, fleshy setae
ventrally on femur, and tarsus, and on both sides of tibia (30–40 µm long). Coxae: I 124–147; II 120–152; III 131–140 µm long; coxa III with at least 4 setae; long setae on coxae not differentiated. Trochanter + femur: I 473–506; II 374–411; III 608–704 µm long; trochanter III with about 3 setae; each trochanter with 3 campaniform sensilla arranged in a line on each side; femur III with about 35 short setae + 4–6 long setae ventrally, with 7 or 8 longer fs on ventral side of femur among shorter setae. Tibia: I 585–649; II 527–562; III 608–704 µm; tibia III with a total of about 100 setae including long setae on both sides of tibia; each distal spur 23–25 µm long. Tarsi: I 164 193; II 142–180; III 148–214 µm long (ratio of length of tibia III to length of tarsus III 1: 0.26); tarsus III with about 23–30 spur-like setae and 2 or 3 long setae ventrally; tarsal digitules very short and setose. Claws fairly long and thin, much longer than width of tarsus (each tarsus about 15 µm long), held at a distinct angle to tarsus, each with 1 small denticle; length: III 40 µm; claw digitules both short and setose.

**Abdomen.** Segments I–VII: tergites and sternites as for family. Setae and lp detected on pleurites (number unknown) but not observable on sternites and tergites. Tubular ducts present in a band of about 20 tubular ducts across tergite VII, each duct 10 µm wide, 20 µm deep, with a slightly spirally-ridged inner surface, probably about 20 tubular ducts. Abdominal spiracles present on anterodorsal part of at least pleurites II–VII. **Segment VIII:** structures as for family, tergite with 1 or 2 pairs of hs dorsal abdominal setae, small locular pores numerous but exact number unknown; sternite with at least 6 setae (probably more but not observable) but no pores; margin rounded, with 2–4 hs pleural setae. With a pair of abdominal spiracles similar to those on more anterior abdominal segments.
Genital segment. Segment X and IX as for family; anus large (40 µm wide). Penial sheath as broad as posterior margin of abdominal segment VIII, short, triangular and blunt; length without segment IX 220 µm, with segment IX 281 µm; greatest width 140 µm; ventrally and laterally with a group of about 15 long hs (each 45 µm long) on each side of anterior end of penial sheath; posteriorly, nearer apex, without minute setae on either surface. Aedeagus shape as for family.

**Orthezia newcomersi** Morrison

(Figures 3.3C; 3.8)

*Orthezia newcomersi* Morrison, 1952: 37.

**Material examined:** USA, California, Sacramento, on *Rubus* sp., 16. v. 1963, R.E. Wilkey coll.: 1/1 adult male (in good condition), housed at the USNM.

**Diagnosis:** Very large body, more than 2.5 mm, large number of loculate pores on dorsal and ventral abdominal segments.

**Description. Mounted material.** Very large, total-body length 2.6 mm. Antennae exceptionally long, nearly 1.7 times total-body length, most segments approximately subequal in length, with numerous short setae; *fs* present on antennae, randomly distributed. Body with few setae, all *hs. Lp* each 11–7 µm wide, with 4–6 loculi, present on both dorsal and ventral surfaces; *smp* each about 3–4 µm wide: sparsely present throughout body.

**Head.** Shape as for family, 435 µm wide and 400 µm long. **Dorsally:** midercranial ridge well developed, extending from midlength of ventromedial part of epicranium dorsally almost to near posterior margin of dorsomedial part of epicranium; ventral arm strong and not bifurcated posteriorly; dorsal arm thinner and fading posteriorly, but with 2 short.
Figure 3.8. *Orthezia newcomeri* Morrison. Adult male. A. Antennal apical seta, B. tarso-tibial connection, C. Claw, D1. Loculate pore with four loculi, D2. Loculate pore with five loculi, D3. Loculate pore with six loculi, E. Tubular ducts with two types of peripheral setae, F. Small locular pores, G. Penial sheath.
branches medially. Dorsomedial part of epicranium sclerotized as for family; with (on each side) 2–3 hs of rather variable length (40–60 µm), all flagellate, plus 1–2 lp and 2–3 mcp. Laterally: Compound eye about 160–175 µm long, with about 120 ommatidia; ocellus 30 µm wide. Ventrally: midcranial ridge and ventromedial part of epicranium as for family; ventral head setae with (on each side) 12–13 hs, 4–6 lp + 6–10 mcp; ventral plate with on each side 2 long hs and 2 lp.

Antenna: segmentation as for family, 4.5 mm long (ratio of total-body length to antennal length 1: 1.73). Scape: 150 µm long, 120 µm wide, each with 7–8 short hs + 1 or 2 minute pores ventrally and 4–6 hs dorsally. Pedicel: length 110–120 µm, width 70 µm; without reticulations or concentric ridges; each with 4–5 fs, 0 or 1 hs, 2–3 minute pores ventrally + a campaniform sensillum dorsally. Segments III–IX all rather long, becoming narrower towards apex, those proximally about 50 µm wide, while apical segment only 25 µm wide: fs between 25–40 µm on all segments, becoming shorter towards apical segment. Lengths of segments (µm): III 633–638; IV 719–727; V 667–684; VI 646–656; VII 601–626 and VIII 474–481; approximate number of setae per segment: III–VIII with about 70–90 fs + 2–9 hs; bristle-like setae absent on these segments. Segment IX elongate: length 472–480 µm; without capitate setae but with about 70 fs + 1 strong terminal bristle, about 25 µm long; coeloconic sensilla not detected.

Thorax. Prothorax. Dorsally: without pronotal ridges and pronotal sclerites; pronotum not observable. Posttergites not identified. Other pronotal setae: dorsally: 1 or 2 hs anterior propleural setae + 3 or 4 lp + about 15 minute pores anteriorly on shoulder; also with a group of posterior propleural setae and pores just anterior to each prealare, extending ventrally and joining antemesospiracular setae: 1 or 2 hs, 15 lp + about 20 smp.
Ventrally: Sternum with a distinct sclerotized median ridge; transverse ridge and prosternal apophyses absent; with 4 hs prosternal setae + 4 lp + 5 smp on each side. Anteprosternal setae absent. Antemesospiracular setae fused with posterior propleural setae. Mesothorax. Dorsally: prescutum quite large, probably rather convex, 230 µm long, 130 µm wide; sclerotized but not nodulated; mesoprephragma shallow; prescutal ridge almost absent, represented by a small sclerotization anterolaterally to prescutum; margin of prescutum and prescutum sutures as for family, without prescutal setae or pores. Scutum sclerotized throughout, without nodulations; distance between prescutum and scutellum medially 130 µm; scutal setae: with about 4 hs + 1 lp + 15 minute pores medially posterior to prescutum and with 1 hs near each lateral margin. Scutellum sub-pentagonal, round anteriorly, very lightly sclerotized, 165 µm wide, 135 µm long; bounded anteriorly by scutoscutellar sutures; without a foramen; scutellum without setae but 4 lp + 4 smp; posterior margin of scutellum represented by a thin ridge, extending laterally along posterior margin of scutum to postalare. Mesopostnotum broad but short, with a rather small membranous area medially as for family; postnotal apophyses well developed. Laterally: prealare quite long and narrow (often present underneath scutum because of the mounted preparation), terminating near mesepisternum; triangular plate absent; tegula sclerotized, with 2 tegular setae + 5 smp. Mesepisternum nodulated near lateropleurite; subepisternal ridge long and well developed. Mesopleural apophyses well developed. Postalare without postalare setae. Mesothoracic spiracle: peritreme almost round, width about 50 µm. Ventrally: basisternum as for family, 525 µm wide, 265 µm long; with a strong median ridge, bounded anteriorly by a narrow, strong marginal ridge which extends down lateral margins; posteriorly, basisternum with a strong precoxal
ridge; with 7 short $hs$ basisternal setae, distributed more or less throughout; lateropleurite as for family broad; furca large, narrow waisted, arms rather broad and very divergent, extending almost to marginal ridge anteriorly. Postmesospiracular setae absent.

**Metathorax. Dorsally:** metapostnotum as for family; metatergal setae in a diffuse band of $4\; hs + 6\; lp + 3\; smp$. Dorsospiracular setae: $3\; hs + 2\; lp + 9\; smp$. Laterally: dorsal part of metaleural ridge well developed, articulating with hamulohaltere; suspensorial sclerite not observed. Metepisternum unsclerotized and without postmetaspiracular setae or pores; a weak precoxal ridge extends anteromedially from posterior end of each metaleural ridge towards posterior spiracle. Metepimeron with a sclerotized ridge running posteriorly, without setae. Antemetaspiracular setae absent. Ventrally: metasternum large and sclerotized, broader anteriorly than posteriorly, with a large subrectangular pit centrally, with strongly sclerotized lateral margins; pit opening into well-developed metafurca; metasternal apophyses present laterally; sclerotized area with $3\; hs + 5\; lp + 10\; smp$ on each side; with 1 $hs$ anterior metasternal setae and 1 or 2 $hs$ posterior metasternal setae. Metathoracic spiracle: peritreme almost round, width 50 $\mu$m.

**Wings.** Shape as for family, 3.0 mm long, about 1.2 mm wide (ratio of length to width 1: 0.39; ratio of total-body length to wing length 1: 1.15; with subcostal ridge extending to less than $\frac{3}{4}$ of wing length, cubital ridge starting 1/8 of wing base; with 4–6 alar setae and a line of at least 30–34 circular sensoria, both along posterior margin of subcostal ridge, extending almost to wing tip; hamulohalteres about 315 $\mu$m long, 38 $\mu$m wide; each with 3 apical hamuli; each 90–95 $\mu$m long.

**Legs.** Relative length as for family. Coxae: I 205–215; II 220–240; III 225–230 $\mu$m long; coxa III with about 5 setae + 3 $smp$. Trochanter + femur: I 865; II 750–755; III 825–845
µm long; trochanter III with about 5 setae; each trochanter with 3 campaniform sensilla
arranged in a line on each side; femur III with about 65–70 setae (ventral ones becoming
spur-like close to tibia) + 25 smp. Tibia: I 1162–1183; II 1021–1059; III 1173–1176 µm;
tibia III with a total of about 100 setae, becoming spur-like on distal half to two-thirds,
particular on ventral side + 13 smp; each distal spur about 40 µm long. Tarsi: I 290; II
287–300; III 282–294 µm long (ratio of length of tibia III to length of tarsus III 1: 0.25);
tarsus III with about 40 setae. Claws fairly long and thin, much longer than width of
tarsus (each tarsus about 30 µm long), held at a distinct angle to tarsus, each with 2 small
denticles; length: III 75 µm; claw digitules both short and setose.

**Abdomen.** **Segments I–VII:** structures as for family. Lp present on both tergites and
sternites, more abundant on sternites II–VI; also fairly numerous on all pleurites. Tubular
ducts present in a single scleritized plate across tergite VII, each duct 15 µm wide; tubular
ducts anteriorly surrounded by fleshy and flagellate setae of two sizes, varying from 10–
65 µm long). Dorsal abdominal setae and pores (totals): segments I–V: 2–4 hs + 20–30 lp
+10 smp; VI 3 hs + 22 lp somewhat fusing to the pleural lp + about 15 smp; VII about 70
fs and 77 tubular ducts and many smp. Pleural setae: dorso- and ventropleural setae
combined on each side: I–VII 4 or 5 hs + 18–25 lp + 15 smp; some setae rather long.
Ventral abdominal setae mostly rather like fleshy setae, each 34–38 µm long (totals): I 2
setae; II 2 setae, 6 lp + 8 smp; III–VI about 12 setae, 15–18 lp + 15 smp; VII 21–25 setae,
5 hs, 0 lp + 0 smp. Abdominal spiracles present on anterodorsal part of pleurites I–VIII,
each peritreme about 10 µm wide, opening into a narrow, inner ductule, before expanding
into a much wider trachea. **Segment VIII:** structures as for family; tergite with 1 pair of hs
dorsal abdominal setae, about 110 small locular pores (different from lp on rest of
abdomen) and many smp; sternite with 25 ventral abdominal setae but no pores; margin rounded, with 3 hs pleural setae, 0 lp + 6 smp.

**Genital segment.** Segment X and IX as for family; anus large (63 µm wide), with a lightly sclerotized area along anterior margin and with 2 hs on tergite IX; sternite IX with 10 setae. Penial sheath narrower than posterior margin of abdominal segment VIII, short, triangular and blunt; length without segment IX 233 µm, with segment IX 300 µm; greatest width 322 µm; ventrally and laterally with a group of 10 or 11 hs on each side of anterior end of penial sheath; posteriorly, nearer apex, without minute setae on either surface. Aedeagus of peculiar shape (uncertain if due to preparation), parallel-sided anteriorly but enlarged at midlength tapering ending as a pointy tip, extending beyond apex of penial sheath; about 257 µm long.

*Praelongorthezia Kozár*


**Generic diagnosis:** Body with loculate pores, mostly 3 or 4 loculi. Head with one short branch on dorsal arm of midcranial ridge, loculate pores absent on dorsal head; ventral micranial ridge with ventral arm strong and bifurcated posteriorly, ventral head setae and loculate pores present; laterally, preoral ridge dorsally long, extending posteriorly or fusing with postoccipital suture, with a short extension medially near each scape; postocular ridge strong dorsally, commencing from dorsal margin of each compound eye and extending posteroventrally along margin of neck; compound eye with more than 100 ommatidia. Prothorax with pronotal ridges and sclerites absent, pronotal, propleural and prosternal setae present; anteprosternal setae absent. Mesothorax with scutal setae rare; scutellum with loculate pores and smp. Wings with with subcostal ridge extending to
more than 3/4 of wing, cubital ridge starting at 1/5 of wing base, alar setae absent; hamulohalteres with 2 hamuli. Legs with long claws, each with a small denticle, claw digitules short and setose. Abdominal tergite VII with two sclerotized plates, bearing numerous tubular ducts, setae on plate concentrated anteriorly, abdominal loculate pores only present on pleurites; sternite IX with a median ridge and few setae; tergite VIII with small locular pores.

*Praelongorthezia praelonga* (Douglas)

(Figures 3.3D; 3.9; 3.10)


**Diagnosis:** As in genus.

**Description. Mounted material.** Total body length 1.85–2.34 mm. Antennae, nearly 1.6 times total-body length, most segments approximately subequal in length, except for last two segments, with numerous setae; fleshy setae present on antennae only. Body with few hs, some setae on legs and abdominal sternites longer and fs-like but here considered to be larger hs; lp each 7–8 µm wide, with 3 loculi mainly, sometimes 4 loculi, present on abdominal pleurites only.

**Head.** Shape as for family, 310 µm wide and long. *Dorsally:* midcranial ridge and dorsomedial part of epicranium as for family, midcranial ridge with one short branch medially, epicranium with (on each side) 4 hs all flagellate, but lp and mcp absent. *Laterally:* Compound eye about 140–200 µm long, with about 130 ommatidia; ocellus 30–40 µm wide. Other lateral structures as described in genus *Ventrally:* midcranial ridge
Figure 3.9. Illustration of *Praelongorthezia praelonga* (Douglas). A. Antennal apical seta, B. tarso-tibial connection, C. Claw, D1. Loculate pore with three loculi, D2. Loculate pore with four loculi, E. Tubular ducts with two types of peripheral setae, F. Small locular pores, G. Penial sheath.
Figure 3.10. Details of cuticular structures on the abdomen of *Praelongorthezia praelonga* (Douglas) from CLSM. **A.** Small locular pores on tergite VIII, **B.** Loculate pores on pleurite, **C.** Tubular pores on tergite VII. Scale bar: 20 µm.
and ventromedial part of epicranium as for family; ventral head with (on each side) 8–12
hs, 1–3 lp + 4–7 mcp. Other ventral structures described as for family.

**Antenna.** Segmentation as for family, long and filiform. Total length 3.31 mm (ratio of
total-body length to antennal length 1: 1.6). Scape: 90–125 μm long, 75–90 μm wide,
each with 3–7 short hs + 1–3 minute pores ventrally and 1 hs dorsally. Pedicel: length
70–83 μm, width 50–62 μm; with 2 fs, 1–4 hs, 1 or 2 minute pore ventrally + 1 (or rarely
2) campaniform sensillum. Segments III–IX with proximal segment 30–45 μm wide,
while apical segment only 18–23 μm wide, with fs 35–40 μm long; lengths of segments
(μm): III 371–458; IV 374–492; V 441–546; VI 462–567; VII 416–472 and VIII 345–
377; approximate number of setae per segment: III–VIII with about 40–60 fs + 4–8 hs.
Segment IX: length 250–444 μm; with about 60 fs + 1 strong terminal bristle, about 40
μm long; coeloconic sensilla not detected.

**Thorax. Prothorax.** Structures as for family, pronotum not observable. Pronotal setae,
with dorsally 1 hs anterior propleural setae anteriorly on shoulder; also with a group of
posterior propleural setae and pores just anterior to each prealare, extending ventrally and
joining antemesospiracular setae: 1 hs + 7–10 lp; median pronotal setae: 2 or 3 fs and
about 5 lp. **Ventrally:** Sternum as for family; with 2–3 hs prosternal setae + 2 lp + 2 smp
on each side. **Mesothorax. Dorsally:** prescutum 130 μm long, 165 μm wide; prescutal
ridges and sutures as for family genus; without prescutal setae or pores. Scutum as for
family; distance between prescutum and scutellum medially 110 μm; scutal setae: with
about 2–4 hs medially posterior to prescutum. Scutellum 165 μm wide, 130 μm long;
without setae but 4–6 lp + 4–8 smp; ridges as for family. Mesopostnotum as for family;
postnotal apophyses well developed. **Laterally:** prealare quite long and narrow
terminating near mesepisternum; tegula sclerotized, with 2 tegular setae. Other structures as for family. Mesothoracic spiracle: peritreme almost round, width about 35 µm.

_Ventrally:_ basisternum as for family, 400 µm wide, 220 µm long; with 6–10 _hs_ basisternal setae; lateropleurite as for family; furca as for family. Postmesospiracular setae absent. **Metathorax. Dorsally:** metapostnotum narrow but reasonably distinct across segment medially; with 2 metatergal setae. Dorsospiracular setae absent. **Laterally:** structures as for family. Metathoracic spiracle: peritreme almost round, width 30 µm.

_Ventrally:_ metasternum as for genus; occasionally with 1 _hs_ anterior metasternal seta and 2 _hs_ posterior metasternal setae + 4 _lp + 6 smp._

**Wings.** Forewing as for family genus, 2.23 mm long, about 805 µm wide (ratio of length to width 1: 0.36; ratio of total-body length to wing length 1: 1.1), with a line of at least 45–50 circular sensoria; hamulohaltere about 220 µm long, 25 µm wide; each with 2 apical hamuli; each 50 µm long.

**Legs.** Relative lengths as for family. Coxae: I 140–160; II 140–171; III 140–171 µm long; coxa III with about 8 setae + 5 _smp_. Trochanter + femur: I 556–697; II 500–608; III 603–722 µm long; trochanter III with about 4 setae; each trochanter with 3 campaniform sensilla arranged in a line on each side; femur III with about 55 setae + 17 _smp_. Tibia: I 820–971; II 719–951; III 910–1088 µm; tibia III with a total of about 120 setae + 10 _smp_; each distal spur 26–30 µm long. Tarsi: I 200–256; II 219–268; III 200–279 µm long (ratio of length of tibia III to length of tarsus III 1: 0.24); tarsus III with about 32 setae Claws much longer than width of tarsus (each tarsus about 15 µm long), held at a distinct angle to tarsus, each with a small denticle; length: III 60 µm; claw digitules both short and setose.
**Abdomen.** *Segments I–VII:* Tergites and sternites as for family. Tubular ducts present in 2 lateral sclerotized plates (about 140 µm long and 80 µm wide) on tergite VII, each duct 7 µm wide; tubular ducts anteriorly surrounded by rather long flagellate setae (20 µm long). Dorsal abdominal setae and pores (totals): segments I–V 4 *hs*; VI 2 *hs*; VII two sclerotized plates with about 20 *hs* and 40–45 tubular ducts on each plate, *hs* concentrated on anterior part of the plates. Pleural setae: dorso- and ventropleural setae combined on each side: I–VII 4–6 *hs* + 6–10 *lp* + 15 *smp*. Ventral abdominal setae mostly rather like fleshy setae, each 36–43 µm long (totals): I 5–7 setae + 1 *smp*; II: 6–9 setae + 1 *hs*; III–VI: 10–14 setae, 1 *hs*; VII: 16–19 setae. Abdominal spiracles present on anterodorsal part of pleurites I–VII, each peritreme about 10 µm wide. *Segment VIII:* tergite with 2 pairs of *hs* dorsal abdominal setae, about 70 *lp* and many *smp*; sternite with 15–20 ventral abdominal setae but no pores; margin rounded, with 4 *hs* pleural setae.

**Genital segment.** Segment X as for family; anus 45 µm wide, with 6 short *hs* on tergite IX; sternite IX with 6–10 setae + 1 or 2 *smp* on each side. Penial, triangular and blunt; length without segment IX 200 µm, with segment IX 265 µm; greatest width 135 µm; ventrally and laterally with a group of 9–15 *hs* on each side of anterior end of penial sheath; posteriorly, nearer apex, without minute setae on either surface. Aedeagus length about 203 µm, structure as for family.

**Comments:** This description is very similar to the description of *Orthezia* sp. from Koteja (1986) and Hodgson and Foldi (2006). However, *Praelongorthezia praelonga* has a unique separation of tergite VII into two sclerotized plates bearing the tubular ducts (Fig. 3.10D).
Genus undetermined

(Figure 3.11)

**Material examined:** U.S.A., Georgia, Spalding county, greenhouse, on *Sarracenia minor*, 15. vii. 1976, H.H. Tippins coll.: 1/1 adult male (in good condition), housed at the USNM. (Labeled as *Orthezia ?graminicola*)

**Diagnosis:** Antennal segments relatively short, with modified capitate setae on each segment, antennal and leg setae sparser than other ortheziid species; loculate pores absent dorsally on head; abdominal loculate pores absent from all sternites and tergites but a few present on pleurites, tubular ducts few on tergite VII, surrounded with very short setae.

**Description:** Mounted material. Large, total-body length 1.4 mm. Antennae long, nearly 1.3 times total body length, most segments approximately subequal in length, with numerous short setae; *fs* present on antennae, randomly distributed. Body with few setae, all *hs*, each with a broad, flattish socket although some setae on legs and abdominal sternites rather long and *fs*-like but here considered to be larger *hs*; *lp* each 9–12 µm wide, with 4–6 loculi; *smp* each about 1–2 µm wide: sparsely present throughout body. Abdomen with loculate pores present only on pleurites; abdominal tergite VII with few tubular ducts.

**Head.** Shape as for family, wider than long, 285 µm wide, 264 µm long, *Dorsally:* midcranial ridge well developed, dorsal arm, strong but fading posteriorly. Dorsomedial part of epicranium and postoccipital suture as for family; with (on each side) 5–6 *hs* of rather variable length (20–30 µm), all flagellate, 3–6 *mcp, lp* absent. *Laterally:* ocular sclerite as for family, compound eye about 115 µm long, with about 110 ommatidia; ocellus 26–27 µm wide
Figure 3.11. Illustration of genus undetermined. A. Antennal apical seta, B. Tibiotarsal connection, C. Claw, D1. Loculate pore with six loculi, D2. Loculate pore with five loculi, E. Tubular duct with peripheral setae, F. Small locular pore.
Preocular ridge as for family; postocular ridge as for family. **Ventrally:** midcranial ridge well developed as for family; ventral arm strong and bifurcated posteriorly; with ventromedial part of epicranium sclerotized but not reticulated; ventral head setae: with (on each side) 6–9 *hs*, 2–3 *lp* + 1 or 2 *mcp*. Other structures as for family. Preoral ridge not detected.

**Antennae.** Shape and segmentation as for family; total length 1880 µm (ratio of total-body length to antennal length 1: 1.3). Scape: 80–84 µm long, 75–82 µm wide, each with 3 short *hs* + 1 or 2 minute pores ventrally and 1 *hs* + 1 minute pore dorsally. Pedicel: 64–68 µm long, 55–57 µm wide; each with 1 *fs*, 4 *hs*, 2 minute pores ventrally + 1 campaniform sensillum dorsally, somewhat removed from distal margin. Segments III–IX all rather long, becoming narrower towards apex, those proximally about 37 µm wide, while apical segment only 18–24 µm wide: *fs* short, those on segment III 22–31 µm long, those on apical segment 27–35 µm long; lengths of segments (µm): III 263–279; IV 292–304; V 263–268; VI 243–271; VII 210–267 and VIII 176–199; approximate number of setae per segment: III–VIII with about 20–30 *fs* + 5–10 long capitate setae (about 50 µm); no bristle-like setae detected on these segments. Segment IX elongate: length 256 µm; with 1 capitate seta and with about 40 *fs* + 1 strong terminal but short bristle, about 15 µm long + 2 subapical capitate setae laterally near apex.

**Thorax. Prothorax.** **Dorsally:** without pronotal ridges and pronotal sclerites; pronotum not observable. Post-tergites each a small, lightly sclerotized, oval area situated mediolaterally. Other pronotal setae: dorsally: 1 or 2 *hs* anterior propleural setae + 1 *lp* on shoulder; also with a group of posterior propleural setae and pores just anterior to each prealare, extending ventrally and joining antemesospiracular setae: 1 *hs*, 5 *lp* + 10 *smp*. 

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Ventrally: cervical sclerites and pleural apophysis as for family. Sternum as for family; transverse ridge and prosternal apophyses as for family; with 2–4 *hs* prosternal setae + 3 *lp* + 2 *smp* on each side. Anteprosternal setae absent. Antemesospiracular setae fused with posterior propleural setae. **Mesothorax. Dorsally:** mesoprephragma as for family; prescutum as for family, 120 µm long, 170 µm wide, prescutal ridge as for family, without prescutal setae or pores. Scutum as for family; distance between prescutum and scutellum medially 68 µm; scutal setae: with about 4 *hs* + 9 minute pores medially posterior to prescutum and with 1 *hs* near each lateral margin. Scutellum as for family, 152 µm wide, 105 µm long, without setae and *lp* but 3 *smp* Mesopostnotum and postnatal apophyses as for family. **Laterally:** prealare as for family (often present underneath scutum because of the mounted preparation), terminating near mesepisternum; tegula sclerotized, with 3 *hs* tegular setae + 2 *smp*. Mesepisternum nodulated near lateropleurite; subepisternal ridge long and well developed. Mesopleural apophyses well developed, each generally with a small area of reticulation. Postalare without postalare setae. Mesothoracic spiracle: peritreme almost round, width about 30 µm. **Ventrally:** basisternum, 434 µm wide, 195 µm long; with a strong median ridge, bounded anteriorly by a narrow, strong marginal ridge which extends down lateral margins; posteriorly, basisternum with a strong precoxal ridge; with 10–12 *hs* basisternal setae, distributed more or less throughout. Postmesospiracular setae absent. **Metathorax. Dorsally:** metapostnotum as for family; metatergal setae in a diffuse band of 1 or 2 *hs*. Dorsospiracular setae: 1 *hs* + 4 *lp* + 5 *smp*. **Laterally:** dorsal part of metapleural ridge well developed, articulating with hamulohaltere; suspensorial sclerite not observed. Posterior part of metapleural ridge well developed. Metepisternum unsclerotized and
without postmetaspiracular setae or pores; a weak precoxal ridge extends anteromedially from posterior end of each metapleural ridge towards posterior spiracle. Metepimeron with a sclerotized ridge running posteriorly, without setae. Antemetaspiracular setae absent. Metathoracic spiracle: peritreme almost round, width 30 µm. *Ventrally:* metasternum as for family, metasternal apophyses present laterally; sclerotized area with 2 *hs* + 3-5 *smp* on each side; occasionally with 2 *hs* anterior metasternal seta and 2 *hs* posterior metasternal setae + 4 *smp.*

**Wings.** Hyaline, 1.6 mm long, about 550 µm wide (ratio of length to width 1: 0.33; ratio of total-body length to wing length 1: 1.17), with subcostal ridge extending to less than ¾ of wing length, cubital ridge starting 1/8 of wing base, posterior flexing patch barely apparent, anterior flexing patch apparent and short; without alar setae but with a line of at least 27–31 circular sensoria along posterior margin of subcostal ridge, the latter extending to 2/3 of the wing total length. Hamulohalteres, each about 212–247 µm long, 35–40 µm wide; with 2 apical hamuli, each 40–50 µm long.

**Legs.** Relative lengths as for family, *fs* not separable from *hs.* Coxae: I 130–136; II 143–147; III 140-148 µm long; coxa III with about 7 setae + 5 *smp*; long setae on coxae not differentiated. Trochanter + femur: I 450–457; II 406–416; III 457–459 µm long; trochanter III with about 3-5 setae; each trochanter with 3 campaniform sensilla arranged in a line on each side; femur III with about 55 *hs* + 11 *smp.* Tibia: I 565–567; II 504–512; III 633 µm; tibia III with a total of about 70 *hs*, these becoming spur-like on distal 1/2 to 2/3 on ventral side + 7 *smp*; spurs on ventral surface of distal end of tibia similar to those more anteriorly; each distal spur 25–30 µm long. Tarsi: I 182; II 174–182; III 185–189 µm long (ratio of length of tibia III to length of tarsus III 1: 0.3); tarsus III with about 25
hs, mainly spur-like. Claws fairly long and thin, much longer than width of tarsus (each tarsus about 20 µm wide), held at a distinct angle to tarsus, each with a small denticle; length: III 48 µm; claw digitules both short and spinose.

**Abdomen.** Segments I–VII: tergites and sternites as for family. *Lp* entirely absent from tergites and sternites II–VI, a few present on all pleurites. Tubular ducts present across tergite VII, each duct 10 µm wide, 15 µm deep. Dorsal abdominal setae and pores (totals): segments I–V 2 hs; VI 2 hs + 2 *smp*; VII about 20 hs and 8 tubular ducts. Pleural setae: dorso- and ventropleural setae combined on each side: I–VII 2 hs + 2–4 *lp* + 2–5 *smp*; some setae rather long, up to 40 µm. Ventral abdominal setae mostly rather like *fs*, each 36–43 µm long (totals): I 5 *fs*; II 9 or 10 *fs*; III–VI 10 *fs*, 3 or 4 *smp*; VII about 15 *fs* + 4 *smp*. Abdominal spiracles present on anterodorsal part of pleurites I–VII, each peritreme about 10 µm wide, opening into a narrow, inner ductule, before expanding into a much wider trachea. **Segment VIII:** tergite as for family, *hs* absent; dorsal abdominal setae, about 35 locular pores (different from *lp* found on rest of abdomen) and many *smp*; sternite with 10 ventral abdominal *hs* but pores absent; margin rounded, with 2 *hs* pleural setae, 0 *lp* + 0–2 *smp*. With a pair of abdominal spiracles similar to those on more anterior abdominal segments.

**Genital segment.** Segment X as for family; segment IX present as an area of sclerotization around anal region and by large sclerotized sternal plate ventrally; anus large (35 µm wide), with a sclerotized area along anterior margin and with 1 or 2 *hs* on tergite IX. Penial sheath as broad as posterior margin of abdominal segment VIII, short, triangular and blunt; length without segment IX 154 µm, with segment IX 209 µm; greatest width 100 µm; ventrally and laterally with a group of 5 *hs* on each side of
anterior end of penial sheath; posteriorly, nearer apex, without minute setae on either surface. Aedeagus as for family, length about 160 µm. Penial sheath with a small group of sensilla on ventral surface near apex on both dorsal and ventral surfaces.

**Comments:** This description is based on one specimen, whose assignement to *Orthezia ?graminicola* was made based on an associated adult female with different collecting information. This specimen, however, displays peculiar features showing that it is not an *Orthezia* species: the number of tubular ducts on tergite VII is very small compared to other *Orthezia* spp., additionally, locular pores are completely absent on both tergites and sternites, with very few setae. The number of setae on the legs is also notably low.

Finally, the antennae present long capitate setae that were never observed in Ortheziidae.

**Discussion**

**Comparisons of extant genera**

The above descriptions of the adult males of seven species adds significantly to the four detailed descriptions previously published (Koteja, 1986; Hodgson and Foldi, 2006). According to the recent revision of the Ortheziidae (Kozár, 2004) based on adult female morphology, these eleven species are now considered to belong to five genera: *Graminorthezia, Insignorthezia, Newsteadia, Orthezia* and *Praelongorthezia*. Based on the above descriptions, the following comments can be made:

(i) This study supports the separation of the following genera *Graminorthezia, Insignorthezia* and *Praelongorthezia* from *Orthezia* (Kozár, 2004) based on male morphology. These three genera differ from *Orthezia* in having a median ridge on abdominal sternite IX, which is absent in *Orthezia.*
(ii) The characteristic differences between *Newsteadia* and other genera, such as the absence of hamulohalteres, reduced number of ommatidia, long setae on the legs and absence of small locular pores on tergite VIII were also found in *Newsteadia americana*. This confirms (until more adult males of *Newsteadia* are found), along with the morphology of adult females, that *Newsteadia* is a distinct lineage within the Ortheziidae. Because *Newsteadia* currently comprises 58 species, descriptions of more adult males might help decipher variation within the genus and possibly reveal diagnostic characters to separate this genus into different taxa, the adult female morphology being relatively uniform (Kozár and Konczné Benedicty, 2000; Konczné Benedicty and Kozár, 2001; Miller and Kozár, 2002).

(iii) The specimen labelled *Orthezia ?graminicola* in the USNM collection (described here as “Genus undetermined”) is peculiar in showing some important differences when compared to the other species of *Orthezia*. “*Orthezia ?graminicola*” lacks (i) multilocular pores on all sternites and tergites and has very few pores on the pleurites; (ii) has fewer than 10 tubular ducts on tergite VII (significantly fewer than in all other known males); (iii) antennal segments III to IX have modified setae resembling capitate setae (Figure 3.11), and (iv) there are significantly fewer setae on the legs than in other Ortheziidae. It is therefore unlikely that this specimen belongs to *Orthezia*. The only other slide associated with this specimen at the USNM (with identical collecting information) is a male prepupa. According to the different handwritings on these slides, the specimens were labelled subsequent to their preparation. A slide containing an adult female and labelled “*Orthezia graminicola*” with the same handwriting is present in the USDA collection but, although from the same state (GA), is from a different county and
was collected on a date prior to that of the males. There is therefore real doubt as to whether these two lots of material are conspecific.

(iv) Specimens described as “Orthezia sp.” by (Koteja, 1986) and “Orthezia sp.” by Hodgson and Foldi (2006) are also unlikely to belong to this genus. Both descriptions are based on specimens collected from Mexico and Colombia respectively. The specimens here described as P. praelonga were also collected in Colombia but the present description differs from both Koteja’s Orthezia sp. and Hodgson and Foldi’s Orthezia sp. in that the tubular ducts on tergite VII are split into two groups (fused in the other descriptions) and loculate pores were not detected on the dorsal part of the epicranium. However, the significance of these differences is uncertain and, given the high overall similarity, it is likely that they are all Praelongorthezia species.

Fossils

The Ortheziidae have traditionally been considered as one of the oldest families of scale insects. Adult females have been described from deposits as young as Dominican amber (ca. 20 My), back to the early Cretaceous, the oldest being from Lebanese amber (see review in Vea and Grimaldi [2012]). To date, adult males have only been described from Lebanese and Baltic ambers. However, a newly discovered piece of Burmese amber, which includes embedded adult males, is under study (Vea and Grimaldi, in prep.)

The oldest adult male assigned to the Ortheziidae, Cretorthezia hammanaica (Koteja and Azar, 2008), was described from Early Cretaceous Lebanese amber and bears 10 antennal segments (only nine segments for Recent species), the apical antennal bristle is absent (present for Recent species) but C. hammanaica has two rather long flagellate setae on the antennal apex, and the genital segment is particularly long compared to the
other described Ortheziidae (fossil and Recent). Even though Koteja and Azar (2008) placed *Cretorthezia* in the Ortheziidae, they expressed doubts as to its relationships with other genera of the family. They also only discussed characters unique to the genus: “small body size, markedly reduced wing venation, entirely reduced halters, long antennae bristles … conspicuous conical, acute penial sheath, about four times as long as wide at base” (Koteja and Azar, 2008: 137). Two other genera, *Palaeonewsteadia* (Koteja, 1987a) and *Protorthezia* Koteja (Koteja, 1987b), were described based on adult male inclusions from Eocene-aged Baltic amber. *Palaeonewsteadia* was considered by Koteja to be a separate genus but closely related to the Recent *Newsteadia*, based on (i) the small body size of *Newsteadia floccosa*, (ii) the few large ommatidia in each compound eye, (iii) the mesosternum with long setae, (iv) the fused trochanter and femur, (v) the long setae on legs, and (vi) the narrow base of the hind wing. However, Koteja drew attention to several significant differences between the fossil and Recent genera, such as (i) the presence of hamulohalteres in *Palaeonewsteadia* (absent in Recent *Newsteadia*) and (ii) an anal fold on the forewing of the fossil. Differences in the genital segments were also noted by Koteja (1987a), who therefore assigned the fossil to a separate genus *Palaeonewsteadia*. Despite the assumption that those two genera are closely related, there is no phylogenetic evidence to support this hypothesis, and further analysis involving Ortheziidae adult male morphology is necessary to assess their relationships. A female specimen from Baltic amber has also been described and assigned at that time to *Newsteadia*. Although there is no possible way to associate specimens of different gender found in the same type of amber (except probably for syninclusions), one can say that the knowledge of the morphological variation of female *Newsteadia* is much
better than for males and so assignment to genera is easier based on fossil female specimens.

*Character interpretation*

The pores on tergite VIII (Fig. 3.10A), described here as small locular pores, are different from the loculate pores on the rest of the abdomen. Hodgson and Foldi (2006) described them as “loculate pores” and Koteja (1986) as “multilocular pores”; both articles treated the pores on tergite VIII as identical to the one on the rest of the abdomen (Fig. 3.10B) However, in CLSM images from this study, these pores are smaller in diameter than the other loculate pores, and although they seem to possess an external ring structure (divided into numerous small compartments), the part surrounded the central loculus is deprived of larger loculi, present in number of 3 to 6 in loculate pores of the rest of the abdomen. On tergite VIII, these locular pores are present in relative abundance across all Ortheziidae (but completely absent in *Newsteadia*), and are surrounded by simple pores; additionally, loculate pores similar to the rest of the abdomen are only present marginally on this tergite (usually few, accompanied by flagellate setae).

Characteristic tubular ducts are always present in the Ortheziidae on tergite VII and often located in a lightly sclerotized band (Fig. 3.10C). These ducts secrete wax filaments, hypothesized to help balance during flight (Gullan and Kosztarab, 1997). In the above specimens of *Praelongorthezia*, the sclerotized band is divided medially in two. The structure of the tubular duct itself seems to be fairly constant across the family, but their frequency and distribution varies between species and genera. For instance, in *N. americana*, there is only a single row, with few ducts. Setae of variable lengths are often present surrounding the tubular ducts, although their distribution differs among species.
These setae are also present in different types; in some cases, they are of one type, thin and very short, as in Genus undetermined (Fig. 3.11E); but on other species, there can be two types, with one very long and fleshy, which appear slightly swollen near their middle and then taper to their apex, and one shorter setae of regular shape, as seen in *Orthezia newcomeri* (Fig 3.8E). Study of more species of more species should clarify whether this character is taxonomically informative.

Hodgson and Foldi (2006) discussed the interpretation of the genital segment in comparison with the aphid and concluded that the penial sheath, aedeagus and basal rod were all derived from segment IX, with the penial sheath having evolved from a paramere-like structure, somewhat similar to that in aphids. Koteja (1986) considered that sternite IX, which is complete in the genus *Orthezia*, is missing in *Newsteadia*. Koteja further hypothesized a transitional phase from the presence of a sternite IX (*Orthezia*), to the presence of a sternite IX with a median ridge (*Praelongorthezia, Graminorthezia*), to finally the loss of sternite IX in *Newsteadia* but with the median ridge remaining and becoming the basal rod. Although there is no direct evidence for this hypothesis, one could look at the relationships between the taxa involved in those three different structures. However, despite the availability of a phylogenetic study of the family based on adult female morphology (Vea and Grimaldi, 2012), there is not enough evidence on the males of other genera to allow optimization of this character on a phylogeny.

The study of scale insects is universally based on observation of material prepared for light compound microscopy. As such, specimens must be typically be prepared meticulously by clearing, staining and fixing, before being mounted in Canada balsam. This reveals good detail of cuticular microstructures (ca. 100 µm and smaller in size) that
are important for the taxonomy of this superfamily. There is a very long tradition of using adult females for the species-level descriptive work, based on their abundance, ease in find them, and thus identification. Major collections of slide-mounted coccoids are comprised of perhaps ≥ 90-95% females. Among the rare slide-mounted adult males in collections, the oldest ones are often uncleared, and, without cuticular transparency, they cannot be properly observed with a standard compound microscopy using transmitted light. Confocal scanning laser microscope (CSLM) is a promising alternative to scanning electron microscope (SEM) in order to obtain highly resolved 3D images of cuticular structures of insects in a medium (Klaus et al., 2004; Böhm et al., 2011). Additionally, this method provides informative scans of opaque, slide-mounted material. For the present study, I obtained CSLM images of two slide mounts of rare Ortheziidae males, Graminorthezia graminis and Orthezia annae, which revealed important structures in 3D rendering that were entirely obscured until full-spectrum light (Figs. 3.1 and 3.5). For instance, in Graminorthezia graminis, the median ridge on sternite IX could be observed using CLSM, but was invisible using traditional light microscopy. However, visibility of cuticular microstructures was still limited with CLSM and many minute pores and setae could not be easily observed. Some abdominal pores and setae were faintly visible by scrolling back and forth between image layers. Finally, scans of properly cleared specimens provided very clear images (Fig. 3.9), revealing structural differences between the loculate and locular pores discussed above. Nonetheless, it was challenging to obtain a clear image on older slides (such as a specimen labeled “?Orthezia graminicola”).
Conclusion

The present study augments our knowledge of male morphology in the Ortheziidae, by providing detailed descriptions of seven more species, representing five different genera. To date, 11 morpho groups have now their males described in this family. Very few mounted specimens are found in coccoid collections. When available, older slide mounts are uncleared, which makes any cuticular observation challenging. Therefore, given the rarity of collected males in this family, we assessed the use of CLSM as a non-destructive method to increase observability of structures for such cases (see Graminorthezia graminis and Orthezia annae). Although this technique improved the observation of ultrastructures (Fig 3.1, 3.5), some cuticular characters, principally pores could not be observed. Because of the difficulty to collect adult males of scale insects in natural habitats, the Ortheziidae presents a particular challenge as, except for a few species, most of the taxa are found in the leaf litter. The author advises that future collected and unidentified adult males be morphologically described in detail, even without immediate species female association. Additionally, obtaining DNA barcodes for newly collected specimens should allow subsequent associations with the females.
References


CHAPTER IV

DIVERSE NEW SCALE INSECTS (HEMIPTERA: COCCOIDEA) IN AMBER FROM THE CRETACEOUS AND TERTIARY AND A PHYLOGENETIC FRAMEWORK FOR FOSSIL COCCOIDEA

(For submission to American Museum Novitates)

Isabelle Vea and David Grimaldi

Abstract

Coccoidea are a major group of phytophagous insects whose diversification is presumed to be associated with the radiation of the angiosperms. Fortunately, coccoids are abundant and diverse in most amber deposits around the world (Tertiary and Cretaceous), but largely as macropterous males. Based on a study of male coccoids in Lebanese amber (Early Cretaceous), Burmese amber (Albian-Cenomanian boundary: 99 Ma), Cambay amber from western India (Early Eocene: 52 Ma) and Baltic amber (mid-Eocene: 44 Ma), 16 new species, 11 new genera, and three new families are herein added to the coccoid fossil record. Moreover, important early records are also provided for six Recent families: Coccidae (in Burmese amber), Diaspididae (in Cambay amber), the first fossil Margarodidae (Cambay), Pityococcidae (Baltic amber), very early Pseudococcidae (Lebanese and Burmese ambers), and Xylococcidae (ibid). The new taxa are the following: Apticococcidae n. fam. based on Apticoccus Koteja and Azar, and including two new species A. fortis n. sp. and A. longitenuis n. sp.; the monotypic family Hodgsonicoccidae n. fam. including Hodgsonicoccus pateactus n. gen., n. sp.; Kozarococcidae n. fam. including Kozarococcus achronus n. gen., n. sp. and K. perpetuus n. sp.; the first occurrence of a Coccidae in Burmese amber, Rosahendersona prisca n. gen., n. sp.; the first fossil record of a Margarodidae sensu stricto,
Heteromargarodes hukamsinghi n. sp.; a peculiar Diaspididae in Indian amber,
Normarkcoccus curtus n. gen., n. sp.; a Pityococcidae from Baltic amber, Pityococcus
moniliformis n. sp., two Pseudococcidae in Lebanese and Burmese ambers,
Eopseudococcus megalops n. gen., n. sp. and Geropseudococcus eukrinops n. gen., n. sp.; an Early Cretaceous Weitschatidae, Pseudoweitschatus audebertis n. gen., n. sp.;
four genera considered as familiae incertae sedis, Alacupacoccus peculiaris n. gen., n. sp., Magnaelentis glaesaria n. gen., n. sp. and Pedicelococcus marginatus n. gen., n. sp. and Priapococcus creticus n. gen., n. sp. A parsimony-based phylogenetic analysis based on 169 morphological characters (both adult males and females) is also presented, along with discussion of some significant characters and relationships of these fossils to extant and extinct groups of Coccoidea.

Introduction

The superfamily Coccoidea is the most diverse lineage of the four major, monophyletic groups of the Sternorrhyncha, the others being Aphidoidea (sister group to the scales), Psylloidea, and Aleyrodoidea (e.g., Börner, 1934; Schlee, 1969; Grimaldi and Engel, 2005). As of 2013, there are approximately 7,900 Recent, described species in 1110 genera and 33 families (Ben-Dov et al., 2013). Since approximately 98-99% of the Recent species feed on angiosperms, they are a group of considerable agricultural and ecological significance. One of the main questions regarding coccoid evolution is: Did the angiosperm radiation have much of an effect, if any, on coccoid evolution?

The wingless, sedentary females and nymphs are the more conspicuous and persistent life history stages of coccoids, either feeding exposed on the surface of their host plants or concealed (in internodes, under bark, and the like), which is why (despite
highly reduced and specialized morphology), the taxonomy of the group is essentially
based on adult females (see Hardy [2013] for a review). Females, however, are rarely
fossilized, notable exceptions being the occasional specimen in amber, as well as Eocene
and Miocene leaves preserved with the remains of female Diaspididae, or armored scales
(Harris et al., 2007; Wappler and Ben-Dov, 2008), a family well known for its durable
encasements.

Males are usually winged (rarely apterous), minute, and ephemeral, and thus
known for perhaps less than 10% of coccoid species. Male coccoids are, however, among
one of the most abundant and diverse groups of insects in amber around the world
(Grimaldi and Engel, 2005), and an excellent insect group for studying evolutionary
changes over the last 130 million years, this being the onset of deposits of highly
fossiliferous amber (Grimaldi and Engel, 2005) and encompassing the period of
angiosperm radiations.

Males are far less reduced in morphology than are females, possessing long,
multi-segmented antennae; eyes (either fully compound, or with isolated facets); a pair of
prothoracic wings; well-developed legs, and sometimes elaborate genitalia. The obvious
apomorphic features of adult male Coccoidea include the absence of functional
mouthparts, well-developed mesothoracic wings with surfaces of varied, diagnostic
textures (the venation is highly reduced to at most subcostal and cubital ridges and
flexing patches), and metathoracic wings reduced to small hamulohalteres (generally with
apical hooked hamuli).

Despite the more complex and generally more informative morphology of males,
comparative studies on them are few (Afifi, 1968; Ghauri, 1962; Giliomee, 1967;
Hodgson et al., 2007; Koteja, 1986a; Hodgson and Foldi, 2006; Theron, 1958; Chapter III in this thesis). However, sufficient comparative information exists among families and the genera of some families to allow phylogenetic placement of fossilized males. Despite the highly biased preservation of coccoids in amber, the earliest fossils of these insects are preserved as compressions. These are *Baisococcus victoriae* Koteja, from the Early Cretaceous (Late Neocomian, ca. 130 Ma) of central Siberia (Koteja, 1989a), and a matsucoccid from the Early Cretaceous Weald Clay of England (Koteja, 1999). The identification of the latter impression (a wing) to a living family was possible because matsucoccids have a very distinctive series of parallel, pinnate grooves on the wing. Other than these few compression fossils, the fossil history of the Coccoidea is preserved in amber.

The present study provides descriptions of 16 new species of fossil coccoids and 14 species-group taxa (genera, families) in Cretaceous and some Tertiary ambers. These descriptions are supported by a morphological phylogenetic analysis, based on 169 characters from both adult females and males, and comprises a total of 123 terminals (73 Recent and 43 fossils). Diagnostic characters and relationships with other Coccoidea taxa are discussed for these new species. These new taxa will be used in the next chapter to estimate divergence time of Coccoidea lineages and how the latter compare to the timing of the angiosperms radiations in the Cretaceous.

*An historical context*

*Early Workers*

Our knowledge of the diversity and systematics of Coccoidea in the fossil record is actually quite good compared to that for most other insect groups, which is due almost
exclusively to the contributions made by Jan Koteja between 1980 and 2004. However, the first reports of scale insects in the fossil record by a coccoid expert date to the beginning of the 20\textsuperscript{th} century (Cockerell, 1906; Cockerell, 1909). Prior to this there were only isolated descriptions of fossil coccoids by 19\textsuperscript{th}-century Germans who worked and published extensively on myriad organisms preserved in Baltic amber (Germar et al., 1856; Koch, 1857). T.D.A. Cockerell (1866-1948) was a natural history polymath who published more than 3,000 papers, on bees (he described some 5,400 species and subspecies of them), scale insects, geology, botany, and fossils in virtually every hexapod order, and was even the author of a volume of poems (Weber, 2000). He was a close colleague of Alfred Russell Wallace and, like him. Cockerell was a gifted and intrepid field naturalist, interested in biogeography and evolution (both men were even born into working-class British families and were socialists at heart). Cockerell became interested in Coccoidea during one of his early positions, as Curator of the Public Museum in Kingston, Jamaica, around which time he made one of his major discoveries in Coccoidea, of the species \textit{Dactylopius opuntiae} (Cockerell, 1896) (Dactylopiidae), a devastating, introduced pest of \textit{Opuntia}. Most of his career was spent at the University of Colorado, where he became fascinated by the vast deposits of Eocene fossil insects from the Green River Formation and at Florissant, Colorado. He undertook the first comprehensive studies of insects preserved in Burmese amber (e.g., Cockerell, 1916; Cockerell, 1917; Cockerell, 1919; Zherikhin and Ross, 2000), a deposit that is of intense interest for researchers worldwide, and a major focus of the present paper. Though modern systematists may be dismissive of these early descriptive works, Cockerell’s insight was remarkable. For example, at that time and up until the 1990’s, Burmese
amber was considered to be Miocene in age (e.g., Rice, 1987; Carpenter, 1992) but, based on the insect taxa Cockerell studied in it, he presciently predicted it to be Cretaceous in age (Cockerell, 1917).

For approximately 60 years after Cockerell had worked on fossil coccoids there was very little research on the subject. For example, Ferris (1957) merely provided comments on species described by Koch, Berendt and Germar. However, Beardsley (1969) then described a species in Late Cretaceous (Santonian-aged) amber from Manitoba, Canada, *Electrococcus canadensis* Beardsley, 1969, which was the first fossil coccoid to be named on the basis of an adult, winged male, as well as the first definitive coccoid from the Cretaceous. By the 1980’s, there was a burgeoning of studies on fossil coccoids, almost all of them by Jan Koteja (see review in Koteja [2000a]).

**Jan Koteja**

Jan Koteja (1932-2004) was a highly talented authority on coccoids at the University of Silesia, Katowice, Poland. His original work on coccoids was entirely morphological and neontological, experience that would provide distinction to his later paleontological studies. Among his most enduring contributions are comprehensive studies on the morphology of coccoid mouthparts (Koteja, 1974a) and appendage sensilla (Koteja, 1974b; Koteja, 1980), work that led to his division of the catch-all family Margarodidae (*sensu* Morrison, 1928) into 10 families (a now broadly accepted classification) (Hodgson and Foldi, 2006; Gullan, 2008). He championed a holistic approach to understanding coccoids, including the study of life histories, nymphs, and males, the last of which are vital to interpreting the coccoid fossil record. Koteja worked with “Benedictine diligence” (Dziedzicka and Podsiadlo, 2008: p. 302) in preparing
meticulous dissections and amber preparations, highly detailed drawings, and his own
catalogue system for some of the 1,700 amber coccoid specimens that he studied (both
borrowed and personally owned). Of the approximately 110 papers Koteja published in
scientific journals on coccoids, 40 of them are on fossils (Veilleux et al., 2013). Given
nearly a millennium of Polish tradition with Baltic amber workmanship (Rice, 1987), it is
hardly surprising that the first episode of Koteja’s “paleococcoid” work involved taxa in
Baltic amber. Those first paleontomological papers provided descriptions of fossil
Matsuococcidae (Koteja 1984; Koteja 1986b; Koteja 1988a; Koteja, 1999) followed by
studies of nymphal and adult males of Eriococcidae and related groups (Koteja, 1988b; c).
He published on Baltic amber fossils of the basal family Ortheziidae, including adult
males (Koteja, 1987a; b) as well as adult females (Koteja and Zak-Ogaza, 1988a; b). A
large study on xylococcid-like taxa in Baltic amber was published posthumously (Koteja,
2008).

The second major episode in Koteja’s study of fossil Coccoidea began in the
1990’s and lasted to his death in 2004. This episode centered on the Cretaceous Period
and was inspired by the discovery of rich new amber deposits as well as a renewed
interest in the Burmese amber. Fossiliferous Cretaceous ambers from Canada and Siberia
had been known for many years, but were barely the subject of study by Koteja. Amber
from Manitoba, Canada, in fact, was discovered as early as the 1930’s (Carpenter et al.
1937), and further outcrops were discovered in southern Alberta in 1963 (McAlpine and
Martin, 1969) (the Alberta amber [Santonian in age, 78-80 Ma] is still being intensively
studied (Pike, 1995; McKellar et al., 2010). Amber from Baikura-Neru and the Maimecha
River of the Taimyr Peninsula (the latter Santonian in age), in northern Siberia, has been
known since the early 1970’s (Zherikhin and Sukacheva, 1973). Despite widespread collaboration among scientists in Poland and the Soviet Union since 1945, Koteja published just one paper on a new species and genus of coccoid in Siberian amber (Koteja, 1988a). A likely reason for this is that Siberian amber, like Canadian amber, has yielded few Coccoidea. Both of these Cretaceous ambers contain abundant Aphidoidea (up to 30% of all inclusions), traditionally explained by the very northerly paleolatitudes when these deposits were formed.

In 1992, a rich outcrop of Turonian-aged (90 Ma) amber was discovered in the Raritan Formation from Sayreville, New Jersey (Grimaldi et al., 2000), containing an exceptional abundance and diversity of coccoids from which Koteja (2000b) described 7 genera and 10 species, placed into 7 families (Table 4.1). This study took Koteja approximately three years because of the abundance of material, and the nature of the Raritan material challenged even Koteja’s considerable preparation skills. Raritan amber is turbid, fractures easily, and many inclusions have a milky coating, such that the amber surface must be ground extremely close to an inclusion, and very slowly.

Soon after the completion of his research on Raritan amber coccoids, Koteja was engaged to study the coccoids in two other deposits of Cretaceous amber, from Myanmar and Lebanon. One involved the collection of Burmese amber at the Natural History Museum in London (NHM) - the very same collection that Cockerell had studied nearly a century earlier. Burmese amber is approximately 99 Ma (Albian-Cenomanian boundary, see below) and, as our present study reveals, the coccoid diversity in this material eclipses even that in the Raritan amber, although individual coccoids are not nearly as abundant in Burmese amber.
Table 4.1. Summary of described fossil Coccoidea, including the species for each genus and family. All deposits are amber unless otherwise stated. Taxa described in this study are highlighted in bold. Deposit abbreviations: Al: Alaska, Bu: Burma, Ba: Baltic, Bi: Bitterfeld, Ca: Canada, Cb: Cambay, DR: Dominican Republic, En: England rock impression, Le: Lebanon, NJ: New Jersey, Si: Siberia rock impression, Ta: Taymir. †: extinct taxon.

<table>
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<th>Species</th>
<th>Deposit</th>
<th>Reference(s)</th>
<th>Life stage</th>
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<td>†Albicoccus</td>
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<td>Bu</td>
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</tr>
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<td>†Apticoccus</td>
<td>minutus Koteja &amp; Azar</td>
<td>Le</td>
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<td>Macropterous male</td>
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Koteja (2004) described three species in three new genera from the Burmese amber collection, but was hampered by NHM restrictions that the material could not be prepared. A one millimeter-sized insect deep inside a slab of amber is impossible to study, so Koteja was relegated to studying only those specimens preserved near the surface. Early Cretaceous amber from Lebanon (see below) was the final subject of Koteja’s fossil research, work that was also published posthumously (Koteja and Azar, 2008). Insect inclusions in Lebanese amber had been known since the 1970’s (Schlee and Dietrich, 1970; Whalley, 1980; reviewed by Azar et al., 2010), but the research of Dany Azar (e.g., Azar, 2000, to present) has made it a major area of focus. Completely opposite to the NHM Collection of Burmese amber, specimens in Azar’s collection of Lebanese amber (presently housed in the Muséum National d’Histoire Naturelle, Paris) are exquisitely prepared for high-magnification study, which greatly facilitated their study by Koteja, particularly since he was terminally ill. One can only imagine Koteja’s sense of urgency and frustration in knowing he would not live to complete his studies of Cretaceous coccoids, a diversity that was scarcely imaginable in 1980.

Present and Future

The continued discovery of new amber deposits will provide abundant new fossil Coccoidea and are likely to transform our understanding of paleodiversity, divergence times, and geneal aspects of coccoid evolution. Since Koteja’s death, four major amber deposits in western Europe have been either discovered or more fully exploited, two of them Eocene and two from the Late Albian, Early Cretaceous. Rovno amber from the Ukraine is similar in age to Eocene Baltic amber (see below) and chemically identical, although it contains species and genera not present in Baltic amber (Perkovsky et al.,
Oise amber from the Paris Basin, France is early Eocene (ca. 53 Ma) and is distinctive for this time period in having been formed by an angiosperm tree (Nel and Brasero, 2010). This may be one reason why the paleobiota in the Oise amber is quite distinct from that in Baltic amber. Late Albian amber from Alava, northern Spain (Alonso et al., 2000; Peñalver and Delclòs, 2010), and Charente-Maritimes, France (Schlüter, 1978; Néraudeau et al., 2002; Perrichot et al., 2010) are major Cretaceous deposits. For none of these deposits, however, have coccoids been studied so far, although few specimens have been found in the Spanish and Charente Cretaceous ambers. New Cretaceous deposits of fossiliferous amber have also been found in Alabama (Eutaw Formation: Santonian; Knight et al., 2010) and Ethiopia (age within the Late Cretaceous uncertain; Schmidt et al., 2012), but the outcrops are still barely excavated. A very rich deposit of early Eocene amber (52 Ma), from the Cambay Shale of Gujarat, India (Rust et al., 2010), see below under Amber Deposits) has exceptional potential for preserving diverse Coccoidea since it was formed under wet tropical conditions by trees in the Dipterocarpaceae, similar to lowland rainforests of southeast Asia today. We describe herein two interesting species in this amber, but the search for arthropod inclusions in this amber is just beginning. Lastly, there is even the possibility that ancient, stem-group coccoids will eventually be found in the mid-Triassic amber from northern Italy (Carnian, ca. 230 Ma), since several minute, foliage-dwelling arthropods have been discovered in this amber (Schmidt et al., 2012).
Material and methods

Amber Deposits

The Coccoidea fossils studied here were derived from four deposits, two of them Tertiary, the other two Cretaceous. One of the two Tertiary deposits is the famous Baltic amber, the world’s largest deposit of amber, which has been exploited for millennia and which has yielded a great diversity of insect inclusions. The review by Weitschat and Wichard (2010) provides a geological context for the Baltic amber, most of which is mined commercially on a large scale on the Samland Peninsula near Jantarnyi, on the eastern shore of the Baltic Sea, Russia. Baltic amber is quite hard and is generally very easy to prepare. Baltic and Burmese amber are available commercially.

The other Tertiary deposit involves Cambay amber from western India. This material was excavated directly by D. Grimaldi, Paul Nascimbene, and Hukam Singh from the Tadkeshwar lignite mines in Surat District, Gujarat state, India. Here, the amber is found in thick lignitic outcrops of the Cambay Shale Formation, dated as earliest Eocene (Ypresian), ca. 52 Ma (see review by Rust et al. [2010], making it slightly older than Baltic amber (Lutetian: ca. 45 Ma [Ritzkowski, 1997]). The Cambay amber is a dammar-type fossil resin, which is poorly cross-linked and which is why the interior of many pieces is slightly soft and sticky. The molecular composition of Cambay and similar fossil resins also allows the material to be completely dissolved (unlike most other types of fossil resins, which are too crosslinked and polymerized). Thus, some inclusions can be extracted from Cambay amber (see fig. 1B and C in Rust et al., 2010), but they are extremely fragile and the extraction requires great care. Because Cambay amber is only partially cross-linked, it requires embedding in a high-quality synthetic
resin (see below), to allow it to be worked and conserved. In proportion to the quantities of Cambay amber preserved in the deposits, exploration for inclusions is still at a very early stage. Without question, this amber deposit will yield a great diversity of Coccoidea.

Burmese amber is the largest Cretaceous deposit of amber in the world, and preserves the most diverse paleofauna of any amber deposit other than Baltic (see reviews by Grimaldi et al., 2002; Ross et al., 2010). It derives from the northern state of Kachin in Myanmar, approximately 100 km west of the town of Myitkyina. Samples of amber matrix from these outcrops were radiometrically dated at 99 Myo using U-Pb isotopes (Shi et al., 2012). This places the age of the deposit very close to the Albian-Cenomanian boundary, which is also the boundary between the Early and Late Cretaceous. Like Baltic amber, Burmese amber is quite hard and easily prepared using conventional techniques but, in general, it is permeated with more fractures (many of which contain veins of calcite).

Lebanese amber is derived from dozens of outcrops throughout Lebanon, from the Late Jurassic to Cenomanian, although only the Cretaceous outcrops have yielded insects (Azar et al., 2010). As discussed by Azar et al. (2010), amber from Jezzine, Bcharreh, and Hammana yield most of the arthropod inclusions. Time control for the material from Jezzine and Bcharreh are not thoroughly established, but known to be Neocomian in age (Valanginian to Hauterivian). The Hammana outcrops are generally Early Aptian in age. Lebanese amber is highly mature and fractures easily; it must be trimmed and polished very carefully, generally requiring epoxy embedding.
**Preparation Methods**

Embedding and preparation techniques followed that of Nascimbene and Silverstein (2000), with some modifications such as use of EpoTek-301 resin for embedding. Grinding used a wet emory paper of decreasing grit sizes (400, 600, 800, 1200, 2400, 4000). Embedding was necessary for pieces with fractures or extremely small pieces. Once embedded, flat surfaces of the amber pieces were carefully trimmed, ground, and polished close to the inclusion (often less than 1.0 mm) so as to maximize dorsal and ventral views of male coccoids, where possible. Flattened amber pieces were temporarily mounted on glass microscope slides with a drop of glycerin; the upper surface of the amber piece was covered with a coverslip also using a drop of glycerin. This method obscures fine surface imperfections and improves resolution at higher magnifications. Coccoid inclusions were studied using reflected and transmitted light (*i.e.*, compound microscopy), at magnifications of generally 100–400x. Because of the minute size of many specimens and the high magnifications required, many amber pieces were trimmed and polished to ca. 2x2x1 mm. In such cases final grinding and polishing was done by hand, gently pressing the minute amber chip against the surface of wet emory paper using the tip of the index finger, and making back-and-forth or circular motions. Drawings were made by first sketching outlines and major structures using a drawing tube attached to a Wild compound scope; details were added using direct observation through this scope at various focal planes, as well as with a Leitz Wetzlar stereoscope at magnifications up to 144x. Measurements were made using ImageJ. In all cases, the length of each structure is its greatest length. Photomicrographs were made using a Nikon D1X digital camera attached to a Nikon Eclipse compound microscope.
generally using 40-100x magnification. Photomicrographic illumination used a fiber optic flash unit (MicrOptics Inc.), generally with transmitted and reflected light and a very narrow diaphragm aperture to improve depth-of-field. It was also necessary to use a series of photomicrographs taken at different focal planes and then z-stacked using the freeware program Combine Z (http://www.hadleyweb.pwp.blueyonder.co.uk/).

Morphological terminology follow previous work by Koteja (e.g., 2000b; 2004).

Material is deposited in the following repositories:

**AMNH**, Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, USA (Burmese and some Lebanese amber specimens);

**BSIP**, Birbal Sahni Institute of Palaeobotany, Lucknow, India (holotypes of Cambay amber);


*Abbreviations for photomicrographs*

abds: abdominal setae

abd: abdomen

ae: aedeagus

afp: anterior flexing patch

aln:alar notch

br: bristle

bs: basisternum

ce: compound eye

c1: claw
cr: cubital ridge
dse: dorsal simple eye
en: endophallus
fe: femur
fws: filamentous wax secretion
ha: hamulohaltere
ham: hamulus
masc: membranous area on scutum
mpnt: mesopostnotum
o: ocellus
osc: ocular sclerite
pe: pedicel
pfp: posterior flexing patch
prsc: prescutum
prnr: pronotal ridge
prtx: prothorax
ps: penial sheath
pt: pterostigma
sc: scape
sctl: scutellum
scr: subcostal ridge
sct: scutum
se: simple eye
td: tubular duct

tds: tubular duct secretion

ti: tibia

tr: trochanter

ts: tarsus

tsd: tarsal digitule

vmr: ventral midcranial ridge

vse: ventral simple eye

_Phylogenetic analysis_

**Taxon sampling**

One hundred fifteen ingroup (Coccoidea) and seven outgroup (Aphidoidea) terminals were selected for the analysis. The total taxon sampling included 72 Recent species and 43 fossil species, representing 48 families of the 54 recognized families in Coccoidea, in addition to the three new families created herein. The complete list of taxa classified into recognized families is provided in Appendix B S4.1.

**Morphological characters**

One hundred sixty nine morphological characters were defined and include 119 characters based on macropterous males and 50 characters from adult females, as listed hereafter. Each species was either coded from specimens in collections of the USNM and MNHN for Recent taxa, AMNH and MNHN for amber inclusions, or the literature (see Appendix Table S1).
Adult male morphology

1. **Number of antennal segments.** 0 = of aphid type; 1 = less than 10 segments; 2 = 10 segments; 3 = more than 10 segments

2. **Relative length of antennal setae.** 1 = longer than antenna diameter; 2 = shorter than antenna diameter

3. **Antennal pedicel enlarged.** 0 = no; 1 = yes

4. **Fleshy setae on antennae.** 0 = present; 1 = absent

5. **Bristles on antennae.** 0 = present; 1 = absent

6. **Reticulations on antennae.** 0 = absent; 1 = present on pedicel; 2 = on other antennal segments

7. **Eyes.** 0 = compound; 1 = simple

8. **Location of the eyes.** 0 = at the same level; 1 = dorsal eyes are found anteriorly relative to ventral eyes; 2 = ventral eyes are found anteriorly relative to dorsal eyes

9. **Relative size of eyes.** 0 = same size for all eyes; 1 = dorsal larger than ventral; 2 = ventral larger than dorsal; 3 = compound eyes

10. **Number of ommatidia or individual eyes.** 0 = between 10 and 50; 1 = between 50 and 100; 2 = more than 100; 3 = seven pairs of eyes; 4 = five pairs of eyes; 5 = three pairs of eyes; 6 = two pairs of eyes; 7 = eight pairs of eyes; 8 = six pairs of eyes; 9 = four pairs of eyes

11. **Functional mouthparts.** 0 = present; 1 = absent

12. **Genae.** 0 = present without setae; 1 = absent; 2 = present with setae

13. **Prothorax.** 0 = sclerotized; 1 = membranous
14. **Shape of the prescutum.** 0=upside-down triangle; 1= elongated oval oriented vertically; 2= triangular with round posterior ridge and separated medially; 3= round; 4= oval elongated horizontally; 5= square

15. **Shape of scutellum.** 0=large rectangle; 1=triangle; 2= subrectangular with round anterior margin; 3= subrectangular with round posterior margin; 5= rhombus; 6= oval; 7= ridges parallel with anterior shorter than posterior margin 8= tubular rectangle

16. **Triangular plates.** 0= absent; 1= present

17. **Tegular setae.** 0= absent; 1= present

18. **Marginal ridge on basisternum.** 0= absent; 1= present and well-sclerotized; 2= present and poorly sclerotized

19. **Wing venation other than the anterior wing ridge.** 0= absent; 1= cubital ridge only; 2= cubital ridge and other veins

20. **Subcostal ridge of fore wing.** 0= extending to the tip of the wing; 1= extending to less than 3/4 the anterior margin; 2= extending to more than 3/4 the anterior margin but not reaching the tip

21. **Pterostigma.** 0= absent; 1= present

22. **Pores on head.** 0= absent; 1= present

23. **Larval eye persistent in adult stage.** 0= dorsally; 1= laterally; 2= absent

24. **Hind wing.** 0= completely absent; 1= modified to hamulohalteres; 2= present and completely developed; 3= reduced but not hamulohalteres.

25. **Postoccipital suture.** 0= absent or reduced; 1= symmetrical Y-shape; 2= asymmetrical Y-shape; 3= curved; 4= linear

26. **Dorsal median crest.** 0= absent; 1= present
27. **Postocular ridge.** 0=absent; 1=present dorsally and ventrally; 2=present only ventrally; 3=present only dorsally

28. **Extension of dorsal midcranial ridge.** 0=extends across whole head and touches the postoccipital suture; 1=doesn't extend to the postoccipital suture; 2=absent; 3=very short

29. **Ventral midcranial ridge.** 0=short; 1=extending to mid length of the head; 2=extending to the posterior part of the head; 3=absent

30. **Preoral ridges.** 0=absent; 1=present

31. **Ventral preocular ridge.** 0=absent; 1=present

32. **Ventral midcranial ridge setae.** 0=absent; 1=present

33. **Ventral midcranial ridge fusion to other ridges.** 0=not fusing; 1=fusing to the preoral ridge; 2=fusing to the lateral preocular ridges

34. **Antennal capitate setae.** 0=absent; 1=present on apical setae only; 2=present on other flagellomeres

35. **Shape of the hind wing.** 0=narrow and long; 1=broad; 2=intermediate; 3=not hamulohalteres.

36. **Ocular sclerite setae.** 0=absent; 1=present

37. **Post-tergites.** 0=absent; 1=present

38. **Dorsomedial part of epicranium.** 0=reticulated; 1=not reticulated

39. **Pronotum.** 0=present and developed as a sclerotized plate around the prothorax; 1=present as a small sclerotization (pronotal sclerites); 2=present as a pronotal ridge only; 3=present as a pronotal ridge and a pronotal sclerite; 4=absent

40. **Pronotal ridge.** 0=absent; 1=curved, U-shaped; 2=short; 3=trilobed
41. **Neck constriction.** 0=absent; 1=strongly marked; 2=slightly marked

42. **Number of hamuli.** 0=absent; 1=one; 2=two or more

43. **Location of the hamuli.** 0=on the anterior ridge of the hind wing; 1=at the tip of the hind wing.

44. **Wings microtrichia.** 0=absent; 1=present

45. **Alar setae.** 0=absent; 1=present

46. **Alar sensoria.** 0=absent; 1=present

47. **Structure holding the hamuli on the forewing.** 0=absent; 1=alar fold; 2=alar lobe

48. **Type of foreleg.** 0=walking; 1=fossorial

49. **Mesoprephragma.** 0=absent; 1=present

50. **Prescutum.** 0=nodulated; 1=not nodulated; 2=absent

51. **Prescutal ridge.** 0=heavily sclerotized; 1=lightly sclerotized; 2=absent

52. **Prescutal suture.** 0=meet medially; 1=do not meet medially; 2=absent

53. **Number of claw digitules.** 0=two; 1=more than two; 2=absent

54. **Scutum.** 0=absent; 1=not nodulated; 2=nodulated

55. **Prescutal setae.** 0=present; 1=absent

56. **Scutal setae.** 0=absent; 1=present

57. **Scutal pores.** 0=absent; 1=present

58. **Foramen.** 0=present; 1=absent

59. **Mesopostnotal apophysis.** 0=well-developed; 1=reduced; 2=absent

60. **Scutellar setae.** 0=present; 1=absent

61. **Scutellar pores.** 0=present; 1=absent

62. **Basisternum median ridge.** 0=strong; 1=weakly sclerotized in parts; 2=absent
63. **Basisternal setae.** 0=present; 1=absent

64. **Number of tarsal segments.** 0=one tarsal segment; 1=two tarsal segments with the one between tibia and tarsal segment 2 reduced; 2=at least two well-developed tarsal segments

65. **Claw digitules protrude out of claw.** 0=no; 1=yes

66. **Type of claw digitules.** 0=hair-like/setose; 1=spine-like/spinose; 2=broadly clavate; 3=thinly clavate; 4=absent

67. **Tarsal digitules.** 0=absent or hair-like (i.e. undifferentiated); 1=present as one pair of thinly clavate digitules; 2=present as more than one pair of thinly clavate digitules

68. **Leg reticulations.** 0=absent; 1=present

69. **Bifurcated setae on profemur.** 0=absent; 1=present

70. **Long flagellate seta on metatrochanter.** 0=absent; 1=present

71. **Claw denticle.** 0=absent; 1=present

72. **Ventral setae on head.** 0=present; 1=absent

73. **Armed-cross on ventral portion of head.** 0=present; 1=absent

74. **Oval membranous areas posterolateral on prescutum.** 0=present; 1=absent

75. **Bifurcated setae on tarsus.** 0=present; 1=absent

76. **Type of tibial spurs.** 0=spinose; 1=clavate; 2=undifferentiated

77. **Lateral extensions on antennal segments.** 0=present; 1=absent

78. **Tubular ducts.** 0=present on tergites VI and VII; 1=present on tergite VII only; 2=present on tergite VI only; 3=absent

79. **Oval membranous areas on scutum.** 0=oval; 1=absent; 2=quadrate ; 3=triangular; 4=lateral areas
80. **Lines of tubular ducts on abdominal segment.** 0=one; 1=more than one; 2=no tubular ducts

81. **Abdominal caudal extension location.** 0=abdominal segments V to VIII; 1=abdominal segment VIII only; 2=absent

82. **Prescutum and scutum.** 0=not distinctly separated; 1=distinctly separated

83. **Cornicles on abdominal segment VII.** 0=present; 1=absent; 2=modified into ostioles

84. **Number of claws.** 0=one; 1=two

85. **Flagellomere structure.** 0=filiform; 1=binodose; 2=trinodose; 3=round

86. **True ocelli.** 0=absent; 1=present

87. **Membranous area on scutellum.** 0=absent; 1=on lateral side only; 2=laterally and medially; 3=only medially

88. **Penial sheath.** 0=triangular; 1=quadrate; 2=spine like; 3=oval; 4=rhombus

89. **Penial setae.** 0=absent; 1=abundant; 2=very few

90. **Relative size of the penial sheath (length divided by base width).** 0=between 0 and 1; 1=between 1 and 5; 2=between 5 and 10; 3=more than 10

91. **Penial sheath apically bifurcated.** 0=yes; 1=no

92. **Satellite setae.** 0=present; 1=absent

93. **Prosternum.** 0=present as a ridge; 1=absent; 2=present as a sclerotized plate; 3=prothorax completely sclerotized

94. **Relative length of caudal extensions.** 0=subequal; 1=increasing in size posteriorly; 2=one caudal extension; 3=absent

95. **Endophallus.** 0=present; 1=absent
96. **Penial sheath position.** 0=anteroventral to anus; 1=posteroventral to anus; 2=protruding out of abdomen

97. **Ratio of wing to antenna.** 0=wing longer than antenna; 1=antenna longer than wing; 2=subequal

98. **Basal rod on aedeagus.** 0=absent; 1=present

99. **Prosternal transverse ridge.** 0=absent; 1=present

100. **Eyes joining ventrally.** 0=yes; 1=no

101. **Prosternal setae.** 0=present; 1=absent

102. **Number of tibial spurs.** 0=two; 1=multiple; 2=one; 3=absent

103. **Base of the wing.** 0=narrow; 1=broad

104. **Apex of the wing.** 0=round; 1=pointed; 2=bilobed

105. **Length of mesopostnotum relative to combined mesothoracic structures**

   (Mesoprescutum + mesoscutum + mesoscutellum). 0=obviously longer; 1=about the same length; 2=shorter

106. **Basisternum furca.** 0=base wide; 1=base narrow; 2=base intermediate in width

107. **Basisternum proportions.** 0=anterior half is subequal to posterior half; 1=anterior half is longer than posterior half; 2=anterior half is shorter than posterior half

108. **Abdominal pleural pores.** 0=absent; 1=present

109. **Abdominal ventral setae.** 0=absent; 1=present; 2=very few

110. **Abdominal ventral pores.** 0=absent; 1=present

111. **Abdominal pleural setae.** 0=absent; 1=present; 2=very few

112. **Abdominal dorsal setae.** 0=absent; 1=present; 2=very few
113. **Abdominal dorsal pores.** 0=absent; 1=present

114. **Pair of long setae on abdomen.** 0=absent; 1=on abdominal pleurite VIII; 2=on pleurites VIII and VII

115. **Number long setae on abdomen.** 0=two setae; 1=multiple setae; 2=one seta; 3=absent; 4=three short setae

116. **Wax filament secretion on at least one abdominal segment.** 0=absent; 1=present

117. **Abdominal spiracles.** 0=absent; 1=very obvious, well developed; 2=obscure, but possibly present and very small (evidenced by the presence of tracheae)

118. **Abdominal spiracle distribution.** 0=all are present (8); 1=more than half; 2=less than half

119. **Glandular group on abdomen.** 0=present; 1=present as a deep pouch; 2=absent

**Adult female morphology**

120. **Number of antennal segments.** 0=less than five; 1=five or six; 2=seven; 3=eight or more; 4=antenna absent

121. **Abdominal crenulations.** 0=absent; 1=present

122. **Anal plates.** 0=absent; 1=one anal plate; 2=two anal plates

123. **8-shaped pores.** 0=absent; 1=present

124. **Legs.** 0=absent; 1=present but reduced; 2=fully developed

125. **Number of tarsal segments.** 0=one; 1=two

126. **Number of claw digitules.** 0=two; 1=more than two; 2=absent

127. **Type of legs.** 0=all walking; 1=fossorial; 2=metathoracic developed and pro- and mesothoracic legs reduced
128. **Claw digitules.** 0=shorter than claw; 1=longer than claw
129. **Bilocular pores.** 0=absent; 1=present
130. **Pores around abdominal spiracles.** 0=absent; 1=present
131. **Anal lobes.** 0=absent; 1=present
132. **Tibia and tarsus.** 0=fused; 1=unfused
133. **Tibio-tarsal articulation.** 0=absent; 1=present
134. **Trochanter and femur.** 0=Fused; 1=Unfused
135. **Pygidium.** 0=absent; 1=present
136. **Anal cleft.** 0=absent; 1=present
137. **Labium segmentation.** 0=one segment; 1=two segments; 2=three segments; 3=four segments; 4=mouth absent
138. **Perivulvar pores.** 0=absent; 1=present
139. **Perispiracular pores.** 0=absent; 1=present
140. **Abdominal spiracles.** 0=absent; 1=between one and four; 2=more than four
141. **Circulus.** 0=absent; 1=present
142. **Trilocular pores.** 0=absent; 1=present
143. **Quadrilocular pores.** 0=absent; 1=present
144. **Tubular ducts.** 0=absent; 1=present
145. **Eye location.** 0=margin; 1=dorsum; 2=venter; 3=eye absent
146. **Type of protection.** 0=no secretion or light white secretions; 1=wax; 2=Diaspididae-like scale cover; 3=unarranged filaments; 4=arranged plates of filaments; 5=lacquer; 6=felt; 7=gall formation
147. **Type of oviposition.** 0=within ovisac; 1=under a protective cover; 2=entirely external; 3=internal marsupium

148. **Reticulations of antennae.** 0=absent; 1=on pedicel only; 2=on other antennal segments

149. **Reticulations on legs.** 0=absent; 1=present

150. **Type of flagellomeres.** 0=round; 1=filiform but all subequal; 2=filiform but with length differences; 3=wider than segment length

151. **Long setae on trochanter.** 0=absent; 1=present

152. **Anal ring.** 0=absent; 1=present with setae; 2=present without setae

153. **Pores on anal ring.** 0=absent; 1=present

154. **Multilocular pores with more than 6 loculi.** 0=absent; 1=present

155. **Pores in peritreme of abdominal spiracles.** 0=absent; 1=present

156. **Dermal papillae.** 0=absent; 1=present

157. **Setae on margin.** 0=absent; 1=present on all body; 2=only present on last abdominal segment

158. **Setae on dorsum.** 0=absent; 1=present; 2=very few

159. **Setae on venter.** 0=absent; 1=present; 2=very few

160. **Spiracular setae.** 0=undifferentiated from marginal setae; 1=differentiated

161. **Cerarii.** 0=absent; 1=present on all segments; 2=present on last abdominal segments only

162. **Ostioles.** 0=absent; 1=present anteriorly and posteriorly; 2=just posterior, as cornicles

163. **Quinquelocular pores.** 0=absent; 1=present
164. **Claw denticle.** 0=absent; 1=present

165. **Relative length of tibia and tarsus.** 0=tibia longer than tarsus; 1=tarsus longer than tibia; 2=tibia and tarsus of subequal length

166. **Cribriform plates.** 0=absent; 1=present

167. **Ovisac band.** 0=absent; 1=present

168. **Shape of trochanter.** 0=small and rectangular (Ortheziidae); 1=triangular but one side round and overlapping femur; 2=triangular (Pseudococcidae)

169. **Pores on atrium of thoracic spiracles.** 0=absent; 1=present

*Parsimony analysis*

The morphological matrix was analyzed using Maximum Parsimony (MP), implemented in TNT (Goloboff et al., 2008). The search was performed as follows: *Acyrthophison* (Aphidoidea) was defined as the outgroup, characters 10, 64 and 105 were ordered (rest of characters treated as unordered) and the tree buffer was set to hold 10,000 trees; the analysis consisted of random addition sequences followed by rearrangements, using TBR swapping and ratchet, 10 trees were held per replication for a total of 1,000 replications (command line: mult=tbr replic 1000 hold 10 ratchet); a strict consensus (Nelsen tree) was obtained; jackknife support values (Farris et al., 1996) with 36% resampling, 1000 replications (command line: resample= jak replic=1000 frequency=36) and Bremer support (Bremer, 1988; 1994) were calculated, and subsequently mapped on the strict consensus tree. Unambiguous characters were mapped using Winclada (Nixon, 2002), and branches without supporting characters were collapsed.
Systematic Paleontology

Order Hemiptera Latreille, 1810
Suborder Sternorrhyncha Duméril, 1806
Superfamily Coccoidea Fallén, 1814

FAMILY WEITSCHATIDAE KOTEJA, 2008

Pseudoweitschatus, new genus

Type species: Pseudoweitschatus audebertis n. sp., by monotypy.


Etymology: The generic name refers to the close similarity of this genus to Weitschatus described in Koteja (2008). Diagnosis: Body large and robust, head with a pair of compound eyes laterally; antennae filiform, each segment, irregularly binodose, almost trinodose, apical segment with curved bristles; dorsal midcranial ridge extending to posterior of head, fusing with postoccipital ridge; prescutum oval; forewings with a subcostal ridge ending by a pterostigma; cubital ridge and posterior flexing patch present; legs slender, with one-segmented tarsus, tarsal digitules absent; claw digitule spinose; dorsal abdominal segments VII and VIII each with a row of 6-9 tubular ducts; penial sheath triangular and short.

Included species: P. audebertis n. sp.

Pseudoweitschatus audebertis, new species

(Figures 4.1; 4.2)

Type locality: Myanmar: Kachin: Tanai Village.

Type: Holotype AMNH Bu-1416 alate male, in a 10 x 8 x 2 mm rectangular,bright orange, transparent polished amber piece; specimen in good condition, but thoracic
Figure 4.1. Photomicrograph of *Pseudoweitschatus audebertis* n. sp. Dorsal surface of holotype AMNH Bu-1416. See Material and Methods for abbreviations.
Figure 4.2. Details of *Pseudoweitschatus audebertis* n. sp. A. Dorsal view of head, B. Ventral view of head, C. Antenna, D. Leg, E. Hamulohaltere, G. Ventral view of penial sheath.
structures significantly shrivelled so the original shapes are uncertain, wings completely
spread with one wing lying on a crack, dorsal tubular secretions directed upward;
accessible views: ventral (but thoracic structures obscured) and dorsal. Myanmar,
Kachin, Tanai Village, on Ledo Road, 105 km NW Myitkyna), Leeward Capitol Corp
coll., deposited in American Museum of Natural History.

Etymology: The epithet is in reference to Vincent Audebert, the first author’s biology
high school teacher, who inspired her to pursue studies in evolutionary biology. This is a
general tribute to scientific educators and their importance in teaching with a passion that
create future scientists.

Diagnosis: As for genus.

Description: Body large and robust, 1.76 mm long, largest width at mesothorax, 465 µm.
Head: transversely rectangular, dorsoventrally flattened, 405 µm wide, 215 µm long.
Each ocular sclerite with a pair of large compound eyes protruding laterally, eye length
ca. 125 µm, each eye with about 100 ommatidia. Ocelli hardly observable but present
dorsad to the compound eyes. Dorsal midcranial ridge well-developed and extending to a
strongly sclerotized postoccipital ridge, setae present on at least on margin of dorsum of
head. Ventral surface of head with ridges forming a five-armed star comprising the
midcranial ridge starting anteriorly and fusing with two preocular ridges and two preoral
ridges.

Antenna 10-segmented and long, total length 1.30-1.33 mm; lengths of segments
(in µm): scape 75-80; pedicel 70-75; flagellar segments III to X all filiform, most
segments irregularly binodose, apical segment the shortest; III 125; IV 180-185; V 180-
190; VI 140-160; VII 135-150; VIII 135; IX 130-135; X 120. All flagellar segments
covered with long setae (110-150 µm), some of them forming whorls of 4 or 9 setae, with few shorter setae (ca. 50 µm) mainly between whorls. Apical segment with 4 or 5 shorter setae curved apically (ca.100 µm) and 4-5 small bristles (ca. 40 µm), and a basiconic sensillum. Capitate setae absent.

Thorax: head and thorax separated by a slight neck constriction. Prothorax well developed but membranous. Ridges on prothorax not observable. Structures of mesothorax shrunken but still differentiable. Dorsally: Prescutum oval (ca. 170 µm wide and 100 µm long), bulging anteriorly, without prescutal setae; scutum without membranous area, scutellum suboval (ca. 165 µm wide, 140 µm long), but anteriorly almost forming a right angle (but it is not sure whether it is due to shrivelling of the thoracic structures), scutellum with strongly sclerotized ridges. Ventral thoracic structures obscured.

Wings: forewing oval, broad at base, almost parallel-sided, with apex tapered, 1.55 mm long and 740 µm widest; subcostal ridge extending from base of wing to more than ¾ wing length, apically forming a distinct club-shaped pterostigma. Cubital ridge starting at 270 µm from wing base and fading before reaching pterostigma level; posterior flexing patch beginning halfway between wing base and cubital ridge; anterior flexing patch less obvious but appearing at same location as cubital ridge but separating progressively. Alar setae absent, sensoria present as a row along subcostal ridge, microtrichia absent. Alar fold present. Hamulohalteres large and elongate, ca. 210 µm long, 50 µm wide; each with four hamuli attached on anterodistal margin.

Legs: slender, all of subequal length, cuticular reticulations absent; coxa ca. 85 µm long; trochanter and femur, 40 µm wide, 305 µm long on proleg, with hair-like setae;
tibia: 342 long µm, 22 µm wide, with short spine-like setae, tibial spurs not differentiated; tarsus one-segmented, 120 µm long, 20 µm wide, setae of same size as tarsal width, tarsal digitules undifferentiated; claw 20 µm, thin and almost uncurved, with two spinose claw digitules, denticle absent.

Abdomen: cylindrical ca. 1.01 mm long (810 µm without penial sheath), 325 µm widest. Tergites and sternites well-developed and segmentation easy to delineate, without caudal extensions on last abdominal segments. Abdominal setae present, short and strong but distribution not clear. Tergite VI and VII each with, one row of 6-9 tubular ducts, extruding wax filaments. Genital segment: penial sheath starting posterior ventrally to anus, triangular, 275 µm long, 80 µm wide at base, narrowing from about ½ length of penial sheath, with short setae present anteriorly. Aedeagus slender and pointed at the apex. Eversible endophallus probably present inside.

Comments: *Pseudoweitchatus* is a xylococcid-like genus, classified here in the family Weitschatidae based the presence of a pterostigma in the forewing, a structure that is otherwise only known in *Weitschatus* among the xylococcid-like genera. However, *Pseudoweitschatus* differs from *Weitschatus* by the latter having a bilobed hamulohaltere and a small caudal extension on tergite VIII (Koteja, 2008). The phylogenetic results retrieves *Pseudoweitschatus* as sister group to *Weitschatus* and the clade including both genera is supported by the round scutellum, the presence of a pterostigma on the forewing, prescutal sutures not meeting medially and the penial protruding out of the last abdominal segment.

Several xylococcid-like taxa were described from Baltic amber but classified into several new families: Arnoldidae, Serafinidae, Weitschatidae, Grohniidae (Koteja, 2008). Koteja
based his generic diagnosis of Xylococcidae on Morrison (1928), with the tribe Xylococcini defined by the presence of a radial sector on the forewing. With this assumption, and the fact that most of the xylococcid-like fossils do not possess this feature, Koteja defined new families for the genera in Baltic amber. Xylococcidae comprises two Recent genera that are so uniform that Hodgson and Foldi (2006) do not even consider that *Xylococcus* and *Xylococculus* have sufficient male morphological differences to be separate genera. Table 4.2 presents a comparison of key characters of xylococcid-like genera, including *Pseudoweitschatus* n. gen. and *Priapococcus* n. gen. (assigned for now as *incertae sedis*). Fossil xylococcid-like taxa were surely much more diverse, even in the Eocene (Koteja, 2008) and further analysis needs to be undertaken to assess whether they are all different genera of one family. Our present phylogenetic analysis did not retrieve the Xylococcidae + other xylococcid-like taxa as monophyletic, due to a lack of resolution, although they appear related, so there is no compelling evidence to synonymize them with Xylococcidae.

**KOZAROCOCCIDAE, NEW FAMILY**

*Type genus:* *Kozarococcus*, n. gen., by monotypy.

*Diagnosis:* Body minute, head large, compound eyes bulging, with less than 100 ommatidia; antenna with filiform segments, capitate and fleshy setae on apical segment; prescutum elongate, without prescutal setae, scutellum triangular; wings hyaline, without microtrichia or pterostigma, with a subcostal ridge extending to ¾ wing length, cubital ridge and posterior flexing patch present; hamulohalteres present, long and narrow; legs slender, tarsus one-segmented, shorter than tibia; claw thin and elongate, almost uncurved, claw digitules slightly clavate, claw denticle absent; abdomen with tubular
Table 4.2. Comparative table of key characters among xylococcid-like taxa

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<td>present</td>
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<td>absent</td>
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<tr>
<td>Pterostigma on forewing</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
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<td>absent</td>
<td>present</td>
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<td>present</td>
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<td>Radial sector on wing</td>
<td>?</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
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<tr>
<td>Hamulohaltere</td>
<td>leaf shape</td>
<td>leaf shape</td>
<td>leaf shape</td>
<td>leaf shape</td>
<td>leaf shape</td>
<td>bilobed</td>
<td>?</td>
<td>leaf shape</td>
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<tr>
<td>Basisternal median ridge</td>
<td>present/light</td>
<td>?</td>
<td>?</td>
<td>?</td>
<td>absent</td>
<td>absent/present</td>
<td>partial</td>
<td>?</td>
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<tr>
<td># clusters of tubular ducts</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
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<tr>
<td>Small caudal extension on tergite VIII</td>
<td>absent</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
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<tr>
<td>Tarsal digitule</td>
<td>undifferentiated</td>
<td>undifferentiated</td>
<td>clavate</td>
<td>undifferentiated</td>
<td>undifferentiated</td>
<td>undifferentiated</td>
<td>clavate</td>
<td>undifferentiated</td>
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<tr>
<td>Penial sheath</td>
<td>short</td>
<td>short</td>
<td>short</td>
<td>short</td>
<td>short</td>
<td>short</td>
<td>elongate</td>
<td>short</td>
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<tr>
<td>Anterior margin of scutellum</td>
<td>round</td>
<td>round</td>
<td>round</td>
<td>pointed</td>
<td>round</td>
<td>round</td>
<td>pointed</td>
<td>?</td>
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<tr>
<td>Lateral areas of scutellum</td>
<td>no</td>
<td>no</td>
<td>yes</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>yes</td>
<td>no</td>
</tr>
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ducts on tergites VII and VIII. Genital segment with exceptionally elongate and apically curved penial sheath.

**Genus included:** *Kozarococcus* n. gen.

*Kozarococcus*, new genus

**Type species:** *Kozarococcus perpetuus* n. sp., designated here.

**Occurrence:** Myanmar: Kachin: near Tanai village. Albian-Cenomanian boundary.

**Etymology:** Patronym in tribute to the recently late Ferenc Kozár, who contributed greatly to the study of scale insects during his distinguished career. Gender: masculine.

**Diagnosis:** As for the family.

**Species included:** *K. perpetuus* n. sp. and *K. achronus* n. sp.

*Kozarococcus perpetuus*, new species

(Figures 4.3A; 4.4)

**Type locality:** Myanmar: Kachin: near Tanai Village (Albian-Cenomanian boundary).

**Type:** Holotype AMNH Bu-1163, alate male, in a 5 x 3 x 0.5 mm yellow, transparent, polished amber piece with several large air bubbles and a crack; specimen in good condition with wings completely spread, tubular secretions visible; accessible views: ventral and dorsal. Myanmar, Kachin, Tanai Village, on Ledo Road, 105 km NW Myitkyna), Leeward Capitol Corp coll., deposited in the American Museum of Natural History.

**Etymology:** The species epithet is the Latin “perpetuus”, meaning “perpetual”.

**Diagnosis:** *Kozarococcus perpetuus* n. sp. differs from *K. achronus* n. sp. by the former having the following characters: antenna 10-segmented (vs. 9 segmented); ocelli absent (vs. present), head without dorsal median ridge (vs. present); basisternal median ridge
Figure 4.3. Photomicrographs of *Kozarococcus* n. gen. A. Ventral surface of *Kozarococcus perpetus* n. sp. holotype AMNH Bu-1163, B. Ventral surface of *Kozarococcus achronus* n. sp. holotype AMNH Bu-233a. See Materials and Methods for abbreviations.
Figure 4.4. Details of *Kozarococcus perpetuus* n. sp. A. Dorsal head, B. Ventral view of head, C. Dorsal view of mesothorax, D. Basisternum, E. Antenna, F. Leg, G. Side view of penial sheath.
completely developed and strong (vs. developed only on posterior half of basisternum); penial sheath longer and thinner, ½ body length (vs. 1/5 ).

**Description:** Body relatively small, total length 1.02 mm, greatest width at mesothorax, 200 µm. Head: transverse; dorsoventrally flattened; width including eyes (245 µm) twice as long as head length (109 µm); with a pair of compound eyes extensively protruding laterally, each eye 105 µm long with 80-90 ommatidia. Ocelli absent. Dorsal midcranial ridge absent. Ventral plate round.

Antenna 10-segmented, total length 480-535 µm; lengths of segments (in µm): scape 35-43; pedicel 50; flagellar segments III to X, all filiform, subequal in length; III 54-62; IV 46-53; V 43-46; VI 48-55; VII 50-65; VIII 55-70; IX 40-50; X 45-55. Setae longer than segment width (10-30 µm). Segment X (apical) bearing 3 capitate setae, 2 curved bristles and ca. 10 hair-like setae of same length as setae of other flagellar segments.

Thorax: head and thorax separated by a strongly constricted neck. Prothorax membranous. Ridges on prothorax not observable. Prosternal ridge present, without lateral extensions. Dorsally: Prescutum oval but longitudinally elongate (75 µm long, 65 µm wide), bulging anteriorly, without prescutal setae; scutum without membranous area; scutellum rhombus-shaped; separated from mesopostnotum by a membrane. Ventrally: Basisternum 112 µm long, 120 µm wide, with a strong median ridge, with setae, anterior part shorter than posterior part.

Wings: both forewings well-preserved, oval-shaped with at wide base, and round apex; 660 µm long, 305 µm at widest section; subcostal ridge extending from base of wing to a little more than ¾ wing length. Cubital ridge and posterior flexing patch.
present. Alar setae, sensoria and microtrichia absent. Alar fold present. Hamulohaltere present, narrow, about 60 μm long; with two hamuli.

Legs: long and slender, cuticular reticulations absent; coxa triangular, coxa length 55 μm long; trochanter and femur 20 μm wide, 160 μm combined length on proleg, with hair-like setae; tibia 148 μm long, 15 μm wide, with hair-like setae becoming spur-like ventrally; tarsus one-segmented, 60 μm long, 13 μm wide, tarsal spurs and digitules undifferentiated; claw thin, 25 μm long, almost uncurved, with two slightly clavate claw digitules, denticle absent.

Abdomen: elongate and narrow, ca. 70 μm at widest section, length without genital segment ca. 210 μm. Tergites and sternites well-developed, segmentation easy to delineate. Abdominal setae not visible. Pores not detected except for tubular ducts. Tergite VII and VIII with each a row of 7 or 8 tubular ducts (tubular ducts not easily observable but wax filaments allow the count of tubular ducts). Genital segment: penial sheath extremely elongate (455 μm long), ⅓ the body length, 35 μm wide. Aedeagus slender, pointed at apex as long as penial sheath. Eversible endophallus absent.

**Kozarococcus achronus**, new species

(Figures 4.3B, 4.5)

**Type locality:** Myanmar: Kachin: near Tanai Village. Albian-Cenomanian boundary.

**Type:** Holotype AMNH Bu-233a, alate male at the edge of a 10 x 10 x 1 mm subsquare, yellow, transparent polished amber piece, specimen in good condition, abdomen transparent, right wing truncated; accessible views: ventral and dorsal. Syninclusions in Bu-233 piece (subsequently separated) include the adult males of an undescribed Ortheziidae, buthid scorpion, and Acari. Myanmar, Kachin, Tanai Village, on Ledo Road,
Figure 4.5. Details of Kozarococcus achronus n. sp. A. Ventral view of head, B. Dorsal view of head, C. Dorsal view of mesothorax, D. Basisternum, E. Apical antennal segments, F. Leg from tibia, G. Dorsal view of posterior abdominal segments and penial sheath, with wax filaments.
105 km NW Myitkyna), Leeward Capitol Corp coll., deposited in the American Museum of Natural History.

**Etymology:** The epithet is from the Greek, “chronos” (time), meaning timeless.

**Diagnosis:** See *Kozarococcus perpetuus* n. sp.

**Description:** Body relatively small, total length 1.13 mm long, largest width at mesothorax, 260 µm. Head: transverse, 280 µm wide, 125 µm long; dorsoventrally flattened. Large compound eyes present, extensively protruding laterally, 120-125 µm wide, each eye with ca. 80 ommatidia. Ocelli present laterally, posterior to compound eyes. Dorsal midcranial ridge present, extending full length of dorsal part of epicranium, fused with postoccipital suture. Ventral midcranial ridge short. Functional mouthparts absent, instead with a round ventral plate.

Antenna 9-segmented, total length 600-640 µm; lengths of segments (in µm):
scape 35-40; pedicel 40-60; flagellar segments III to X, all filiform, of subequal length;
III 60-80; IV 80-90; V 75-85; VI 80-85; VII 80; VIII 60-75; IX 50-80; with 10-15 setae subequal to segment width. Apical segment bearing 3 capitate setae, 2 curved bristles and ca. 10 hair-like setae of same length as other flagellar segments.

Thorax: head and thorax separated by a well-developed neck constriction.

Prothorax well developed and membranous. Ridges, setae and pores on prothorax not observable. Prosternal ridge present, without lateral extensions. Mesothorax dorsally: Prescutum very elongate, bulging anteriorly, without setae; scutum without membranous area, scutellum of subrhombus shape; separated from mesopostnotum by a membrane.

Ventrally: Basisternum 160 µm long, 160 µm wide, with a median ridge only present posteriorly. Anterior part of basisternum shorter than posterior part.
Wings: forewings both well preserved, oval with an intermediate width at base, apex rounded; 845 \( \mu m \) long, 90 \( \mu m \) widest; subcostal ridge extending from base of wing to a little more than \( \frac{3}{4} \) wing length. Cubital ridge and posterior flexing patch present. Alar setae, sensoria and microtrichia absent. Alar fold present. Hamulohalteres present, long and narrow, 90 \( \mu m \) long, with two hamuli.

Legs long and slender, cuticular reticulations absent. Prolegs: coxa triangular, 55 \( \mu m \) long; trochanter and femur about 27 \( \mu m \) wide, together 200 \( \mu m \) long, with hair-like setae, tibia 105 \( \mu m \) long, 16 \( \mu m \) wide, with hair-like setae becoming spine-like ventrally; tarsus one-segmented, 40 \( \mu m \) long, 14 \( \mu m \) wide, tarsal spurs and digitules undifferentiated; claw thin, 20 \( \mu m \) long, claw digitules or denticles not observed.

Abdomen: broad (370 \( \mu m \) long without genital segment; 200 \( \mu m \) widest). Tergites and sternites well developed, mostly membranous, segmentation easy to delineate. Abdominal setae not observed despite abdominal transparency. No pore detected except for tubular ducts. Tergite VII and VIII, each with a row of ca. 10 tubular ducts. Genital segment: penial sheath extremely elongate (about 255 \( \mu m \) long), about 1/5 body length, 60 \( \mu m \) widest, proximally and distally enlarged and medially narrow; aedeagus slender and pointed at apex. Eversible endophallus absent.

Comments: *Kozarococcus* shows some similarity to *Matsucoccus* Cockerell (Matsucoccidae). The head structure overall resembles that of *Matsucoccus*, especially the general shape, the apical flagellar segment bearing capitate setae and curved bristles, the protruding compound eyes, and the short mesopostnotum. However, there are obvious other features that differ significantly from *Matsucoccus*: the presence of tubular ducts on segments VII and VIII (vs. only present on segment VI in *Matsucoccus*), the long penial
sheath, the significantly smaller body size, the proportions of the abdomen, and the presence of setae and a strong median ridge on the basisternum (vs. basisternal median ridge present or absent, and setae absent). Matsucoccidae is one of the most homogeneous families (one extant and one fossil genus), the males of which are easily recognized by their wing membrane structure bearing parallel pennate ridges. This distinctive wing structure is even preserved as an impression in sedimentary rock, representing the oldest definitive coccoid (Koteja, 1999). Matsucoccidae are common in Eocene Baltic amber (Koteja, 2000). Interestingly, this “herring bone” wing membrane pattern is very conserved, showing little variation amongst Recent and fossil Matsucoccidae. Based on the significantly different wing type and tubular duct distribution that is more similar to other archeococccoid families, Kozarococcus can be excluded from the Matsucoccidae. Additionally, the morphological phylogenetic analysis retrieved Kozarococcidae as monophyletic and is included in a clade comprising the Xylococcidae and related extinct families of Koteja (2008), Lebanococcidae, and Alacupacoccus n. gen., described here as incertae sedis. Kozarococcidae appears to be a sister group to Alacupacoccus and Lebanococcidae Despite the rough similarity to Matsucoccidae, Kozarococcus is not related to this family.

FAMILY MARGARODIDAE COCKERELL

*Heteromargarodes*, Jakubski

**Type species:** *Heteromargarodes americanus* Jakubski, 1965.

**Occurrence:** Recent distribution in the Nearctic. Fossil in Cambay Formation of India.

Species included: This recent genus was defined based on adult female morphology and includes the Recent *H. americanus*, *H. chukar* (La Rivers) and *H. hiemalis* (Cockerell). Only the adult male of *H. americanus* has been described (Hodgson and Foldi, 2006).

*Heteromargarodes hukansinghi*, new species

(Figures 4.6; 4.7)

Type locality: India: Gujarat: Tadkeshwar lignite mine. Cambay Formation (Paleo-Eocene).

Type: Holotype Tad-139, alate male in a piece of 10 x 5 x 1.5 mm rectangular, yellow, transparent, polished amber, with a crack, air bubbles and soil debris; specimen is adjacent to debris so a dorsal view is obstructed, apices of antennae are truncated, wings spread but somewhat folded; accessible view: ventral. India: Gujarat: Tadkeshwar lignite mine, Cambay Formation (Paleo-Eocene/7-12/2009, Grimaldi and Nascimbene, coll., deposited in Birbal Sahni Institute for Palaeobotany, Lucknow, India.

Etymology: Patronym for Hukam Singh, Birbal Sahni Institute for Palaeobotany, Lucknow, for his valuable work on the paleobotany of the Cambay Shale, including its amber.

Diagnosis: Differs from the male of *Heteromargarodes americanus* described in Hodgson and Foldi (2006) based on the following characters (characters for *H. americanus* in parentheses): leg setae spinose (vs. hair-like), large bristles on flagellar segments absent (vs. present), penial sheath longer.

Description: Body large, robust, parallel sided, total length 1595 µm, largest width 322 µm. Head broadly oval, 200 µm wide, 200 µm long; with elongate compound eyes, not protruding from head, almost meeting ventrally, eye length ca. 160 µm, each eye with ca.
Figure 4.6. Photomicrographs of *Heteromargarodes hukamsinghi* n. sp. **A.** Ventral surface of holotype AMNH Tad-139, **B.** Enlarged ventral view of head and thorax. See Materials and Methods for abbreviations.
Figure 4.7. Details of *Heteromargarodes hukamsinghi* n. sp. A. Ventral view of head, B. Antenna, C. Fore leg, D. Hind leg, E. Ventral side of penial sheath.
30-40 large ommatidia. Ocelli not visible, but probably present. Dorsal ridges, if present, not observable. Ventrally with a well-developed mid-cranial ridge, extending to and meeting compound eyes.

Antenna at least 9-segmented (apical segments lost on holotype); lengths of segments (in µm): scape 70-75, with less than 10 strong setose setae; pedicel 60-68, with numerous hair-like setae; flagellar segments III to IX all relatively short, narrower proximally, enlarged distally, subequal in length, 70-80 µm. All flagellar segments covered with numerous hair-like setae, each 25-30 µm long.

Thorax: head and thorax without neck constriction. Prothorax well developed but membranous, setae visible laterally (no other thoracic sclerites not visible dorsally or ventrally due to debris and darkness of amber).

Wings: forewings oval, of intermediate width at base, ca. 1.00 mm long and 570 µm at widest section; subcostal ridge extending from base of wing to more than ¾ wing length, terminating at well-developed pterostigma, with a cubital ridge and anterior and posterior flexing patches; large alar fold present. Alar setae and sensoria not visible. Microtrichia absent. Hamulohalteres present but folded, number of hamuli not identifiable but probably present.

Legs robust, cuticular reticulations absent, prolegs fossorial. Prothoracic legs: coxa not visible; combined length of trochanter + femur 215 µm, 88 µm wide, with hair-like setae, bifurcated setae absent. Tibia 90 µm long, 45 µm wide, with hair-like setae becoming spine-like ventrally (tibial spurs), bifurcated setae absent; tarsus one-segmented, 42 µm long, 35 µm wide, tarsal digitules absent; claw large 50 µm thick, claw digitules spinose, claw denticle absent. Meso- and metathoracic legs of subequal length:
coxa elongate, 130 µm; trochanter + femur 245 µm, 73 µm widest, with numerous hair-like setae, bifurcated setae absent; tibia 210 µm, with numerous spine-like setae and tibial spurs on ventral margin, bifurcated setae absent; tarsus 82 µm, with spine-like setae, with a longer ventral setae along tarsus; claw thin, uncurved, 55 µm, digitule spinose, extending along claw but not protruding, claw denticle absent.

Abdomen: cylindrical, ca. 660 µm long (515 µm without penial sheath), 310 µm widest, parallel-sided and slightly tapered posteriorly (abdomen is partially concealed by a white coating). Abdominal setae visible on posterior segments, with groups of 4 or 5 setae (40-75 µm long) on segment VII and VIII. Dorsal structures not visible.

Genital segment: penial sheath originating ventrally on tergite VII, subquadrate, tapering posteriorly, 140 µm long, 85 µm wide at base, possibly bifurcate apically. Aedeagus slender and round at apex. Eversible endophallus not visible.

Comments: Heteromargarodes hukamsinghi n. sp. is placed within this genus based on the description of the adult male of Heteromargarodes americanus. Hodgson and Foldi (2006) also described a specimen probably belonging to Heteromargarodes chukar (La Rivers). The latter species was originally described in Margarodes, but was transferred in Heteromargarodes based on female morphology, as presented in Unruh and Gullan (2007). Given the morphological variation amongst genera in Margarodidae sensu stricto provided in Hodgson and Foldi (2006), Heteromargarodes is the probable genus to which H. hukamsinghi n. sp. belongs because of the general shape of antennal segments, being each more enlarged proximally (this feature is found in H. americanus although in H. chukar the antennal segments are significantly shorten); the shape of compound eye, almost forming a plate surrounding the head (most resembling H. americanus); the legs
have a more slender appearance, with the fossorial prolegs not extremely shorter than the meso- and metathoracic legs; and by the absence of bifurcate setae on the legs. The phylogenetic analysis retrieved *H. hukamsinghi* n. sp. within the family Margarodidae. However, there is no resolution of the fossil and genera of Margarodidae that were sampled. This fossil is highly significant in that it is the first occurrence of the family Margarodidae *sensu stricto* in the fossil record.

**HODGSONICOCCIDAE, NEW FAMILY**

**Type genus:** *Hodgsonicoccus* n. gen., by monotypy.

**Diagnosis:** Body large (ca. 2 mm), head with two ocular sclerites, each bearing less than 20 large and protruding simple eyes; antenna long, with binodose flagellar segments, each with long setae organized in whorls, each becoming shorter distally; forewings elongate and narrowed apically, subcostal ridge extending to tip of wing, cubital ridge present, membrane with microtrichia; hamulohaltere large and broad, with microtrichia, three hamuli inserted on anterior margin; abdomen with several long, spinose setae on posterior segments; penial sheath triangular, with a large, everted endophallus.

**Genus included:** *Hodgsonicoccus* n. gen.

*Hodgsonicoccus,* new genus

**Type species:** *Hodgsonicoccus patefactus* n. sp., by monotypy.

**Occurrence:** Lebanon: North Lebanon: Bchare Mountain. Early Cretaceous.

**Etymology:** The genus is named for Christopher J. Hodgson, who has contributed immensely to our understanding of the adult male morphology of coccoids, especially in the lesser known families. Gender: masculine.

**Diagnosis:** As for the family.
Species included: *H. patefactus* n. sp.

*Hodgsonicoccus patefactus*, new species

(Figures 4.8; 4.9)

**Type locality:** Early Cretaceous, Lebanon, North Lebanon, Bchare Mountain,

**Type:** Holotype AMNH LAE-93, alate male in a 8 x 2.5 x 2 trimmed and polished amber piece, embedded in epoxy, specimen in good condition but lying on a crack and surrounded on the dorsal and ventral surfaces by a large air bubble; accessible views: lateral and partial ventral and dorsal. North Lebanon, Bchare Mountain, 2300 m, Antoni Estephan coll., deposited in the American Museum of Natural History. Syninclusion: undescribed second or third instar nymph of undescribed Coccoidea.

**Etymology:** The epithet is from the Latin nominative of “pactefactus”, meaning “disclosed, opened”.

**Diagnosis:** As for genus.

**Description:** Body large, total length 2.04 mm, largest width at mesothorax, ca. 500 µm.

Head: short, 290 µm wide, 185 µm long, with well-developed ocular sclerites surrounding most of head, bearing 10-15 large, simple eyes. Ocelli present dorsally. Head ridges not observable.

Antenna 10-segmented; long, total length 1.56 mm, segments III-X binodose; antennomere lengths (in µm): scape ca. 100-110; pedicel 130; III 190-195; IV 180-185; V 190-200; VI 180-185; VII 150-160; VIII 130-135; IX 110; X 120-130. Setae long, organized on each segment in whorls, each setal length decreasing towards apical segment (300 µm for setae on proximal segments to 90 µm for apical segment). Apical segment also bearing basiconal setae and curved bristles.
Figure 4.8. Photomicrograph of *Hodgsonicoccus patefactus* n. sp. A. Lateral side of holotype AMNH LAE-93, B. Antennae, C. Head and thorax from lateral side, D. Lateral side of penial sheath.
Figure 4.9. Details of *Hodgsonicoccus patefactus* n. sp. A. Head from right lateral view, B. Antenna, C. Tarsus and claw, D. Fore wing, E. Hamulohaltere, F. Left lateral side of penial sheath.
Thorax: head and thorax not obviously separated. Prothorax membranous. Ridges on prothorax not observable. Dorsally: Prescutum suboval, not obviously separated from scutum, with setae; scutum with a medial membranous area extending from prescutum to scutellum; scutellum round; mesopostnotum well developed. Ventral prothoracic structure not visible; basisternum large, with a median ridge, setae not observed.

Wings: forewings elongate, with narrow base, apex narrowed, 2.22 mm long, 800 µm widest; subcostal ridge extending from wing base to tip. Cubital ridge present and originating from base, 1/10 wing length, extending to 7/10 wing length. Alar setae and sensoria present on subcostal ridge, minute microtrichia present throughout wing surface. Alar fold present. Hamulohalteres large, ca. 290 µm long, 85 µm wide; with microtrichia, with 3 hamuli located on anterior margin of hamulohaltere.

Legs: long, slender but robust, all of subequal length, cuticular reticulations absent; prolegs: coxa triangular, elongate, 185 µm long; trochanter and femur, 550 µm long, 50 µm wide on proleg, with numerous strong hair-like setae, with a few bifurcated setae; tibia: 470 µm long, 30 µm wide, with strong hair-like setae becoming spine-like ventrally and bifurcate; tarsus two-segmented, 180 µm long, 30 µm wide, tarsal spurs and digitules undifferentiated; claw thin, 40 µm long, virtually uncurved, with spinose claw digitules, denticle absent.

Abdomen: elongate, 795 µm long (580 µm without genital segment), dorsoventrally flattened (about 70 µm widest), parallel sided, tapered posteriorly. Abdominal segments bearing numerous setae, with posterior segments having 10-15 long, stiff, spine-like setae (300-500 µm long). Caudal extension absent. Genital segment:
penial sheath triangular. Aedeagus slender and pointed at apex; eversible endophallus present.

Comments: This new family is very distinctive due to its size, compared to all other fossil coccoids known from Lebanese amber, which are otherwise all minute. Additionally, the eye structure is unique with a potential intermediate state between a well-developed compound eye and separate but multiple simple eyes; the combination of wing structure, binodose antennae, and multiple long spinose setae on the abdomen is unknown amongst Coccoidea. The hamulohaltere bears microtrichia and the hamuli are inserted on the anterior margin, suggesting a plesiomorphic condition. Finally, bifurcated setae, present on the femur and tibia, are only present in some Margarodidae, Stigmacoccidae, Kuwaniidae and in all Monophlebidae and Coelostomidiidae (Hodgson and Foldi, 2006), not none of these families have the combination of characters found in Hodgsonicoccus. The most similar fossil that could be associated with Hodgsonicoccus is Jersicoccus Koteja. Jersicoccus has a similar wing shape and binodose antennae, but it differs by having compound eyes with numerous ommatidia and waxy filaments on the abdomen. The phylogenetic results retrieved Hodgsonicoccus as sister genus to Jersicoccus (Jersicoccidae) described from New Jersey amber (Koteja, 2000b), but the former was not classified in Jersicoccidae because of the peculiar ocular sclerites. Finally, Hodgsonicoccus and Jersicoccus were together retrieved as sister to all Recent Coelostomidiidae and Monophlebidae.
FAMILY PITYOCOCCIDAE MCKENZIE

*Pityococcus* McKenzie, 1942

**Type species:** *Pityococcus ferrisi* McKenzie, 1942


**Occurrence:** Recent species distributed in the Nearctic. Fossil species in Baltic amber.

**Species included:** *Pityococcus* was described based on adult female morphology and includes the Recent *P. deleoni* McKenzie, *P. ferrisi* and *P. rugulosus* McKenzie. Only an unidentified *Pityococcus* was described based on a macropterous male in Hodgson and Foldi (2006).

**Pityococcus moniliformis**, new species

(Figures 4.10; 4.11)

**Type locality:** Baltic amber; Palmnicken mines in Yantaryni, on the eastern coast of the Baltic Sea, Russia. **Type:** Holotype AMNH Ba-Ve762, alate male in a 5 x 5 x 1 mm square, light orange, transparent polished amber piece; specimen in good preservation with some internal organs visible through transparent cuticle, lying on a layer, with one wing well spread and onefolded, white milky layers obstructing some parts, such as the head area; accessible views: ventral and dorsal. Baltic amber, Palmnicken mines in Yantaryni, on the eastern coast of the Baltic Sea, Russia. Purchased from Jurgen Velten Baltic amber collection. Deposited at the American Museum of Natural History.

**Etymology:** The epithet *moniliformis* is composed of the Latin dative of “monile”, meaning “necklace” or “collar” and the Latin dative of “forma” (f), meaning “shape”. This refers to the round, bead-like antennal segments.
Figure 4.10. Photomicrograph of *Pityococcus moniliformis* n. sp., holotype AMNH Ba-Ve762
A. Dorsal surface, B. Ventral surface.
Figure 4.11. Details of Pityococcus moniliformis n. sp. A. Dorsal view of head, B. Ventral view of head, C. Dorsal view of mesothorax, D. Basisternum, E. Antenna, F. Leg, G. Ventral view of penial sheath.
**Diagnosis:** *Pityococcus moniliformis* differs from *Pityococcus* sp. in Hodgson and Foldi (2006) by the following characters: length of antennal segments proportionally shorter than *Pityococcus* sp. (Hodgson and Foldi, 2006); large bristle on antennal segment VIII absent (vs. present); tarsal digitule finely clavate and long (vs. absent).

**Description:** Body small, total length 1.13 mm long, widest at mesothorax, 315 µm.

Head: almost round, 205 µm wide, 145 long. Dorsal median crest absent, postoccipital suture absent, setae not observed. Ocular sclerite broad, extending as a wide lateral band and meeting ventrally; ocular sclerite with five pairs of simple eyes along anterior margin; ventral and dorsal eyes larger than lateral eyes (30 µm and 20 µm wide respectively), ventral eyes not joining medially; ocelli present laterally. Ventral part of epicranium with wide ventral medial crest, with ca 10 setae. Setae also present on the rest of ventral part of epicranium, anteriorly. Ventral midcranial ridge present, extending to posterior end of head.

Antenna 9-segmented, total length 305-375 µm; lengths of segments (in µm)

- scape 25; pedicel 50; flagellar segments III to X all filiform, subequal in length; II 30-45; IV 35-45; V 35-45; VI 35-40; VII 30-45; VIII 30-40; IX 35-40. Each segment with hair-like setae (15-20 µm long) and very short fleshy setae (6-10 µm long), all shorter than segment width. Apical segment with 4 capitate setae (ca. 35 µm), 3 large bristles (25-30 µm) and some hair-like setae of the same length as on other flagellar segments.

Thorax: head and thorax separated by a slight neck constriction. Prothorax well developed but membranous. Prosternal ridge present, bifurcating posteriorly, with a pair of setae. Dorsally: Prescutum strongly sclerotized, oval and broad (124 µm wide, 77 µm long), not completely separated from scutum, setae difficult to see. Scutum with a pair of
membranous areas laterally. Scutellum quadrangular, anterior margin shorter than posterior margin, 55 µm long, 85 µm (anterior margin) to 140 µm (posterior margin) wide, divided by a median ridge, with a pair of scutellar setae. Ventrally: basisternum (135 µm long, 175 µm wide) without a median ridge, with ca 20 basisternal setae. Anterior part of basisternum shorter than posterior part.

Wings: oval, with a medium base, distal width smaller than proximal width; 780 µm long and 415 µm widest; subcostal ridge extending from the base of the wing to more than ¾ wing length. Only cubital ridge present. Alar setae and sensoria not observed, microtrichia present across wing surface Alar lobe present. Hamulohalteres not detected, but probably present.

Legs: subequal in length, cuticular reticulations absent; prolegs: coxa triangular, 50-60 µm long, trochanter and femur fused, 145-155 µm long, with hair-like setae; tibia: 80-90 µm long, with hair-like setae becoming spine-like ventrally; tarsus two-segmented, 85 µm long, tarsal digitules present and thinly clavate; claw thin but strong, 25 µm long, with spinose claw digitules, denticle present.

Abdomen: cylindrical (505 µm long, 365 µm long without genial segment; 170 µm widest). Tergites and sternites well developed, mostly membranous, segmentation easy to delineate. With a pair of long setae on each side of each abdominal segment dorsally, a few short setae ventrally. Ostioles detected on abdominal segment VI by a slight enlargement on posterior part. Glandular pouches not directly observed. Genital segment: penial sheath small (65 µm wide, 105 µm long), almost parallel sided anteriorly for more than ½ of length, with few short setae. Aedeagus broader than tip of penial sheath. Endophallus everted, covered with small spines.
Comments: Adult males of *Pityococcus* have been frequently found as inclusions in Eocene ambers. However, according to Koteja (2000a), they are apterous. Therefore, this is the first formal description of a winged male *Pityococcus* in the fossil record. There are currently three described extant *Pityococcus* spp., all of which are based on adult females. Hodgson and Foldi (2006) provided the only description of a macropterous male *Pityococcus*, but unidentified to species. The same authors also mentioned a specimen of *Pityococcus* labeled as *P. deleoni* McKenzie but most appendages were missing. *Pityococcus moniliformis* n. sp. was assigned in this genus by the following combination of characters: a row of five simple eyes; antennae bearing short, stout, fleshy setae; the presence of capitate setae; the presence of a membranous area on the scutum; the quadrangular shape of the scutellum, with anterior margin shorter than posterior margin, and the presence of ostioles on abdominal segment VI. In the phylogenetic analysis, *P. moniliformis* is retrieved as the sister taxon of the Recent *Pityococcus* sp., the node of which is defined by the presence of ostioles on abdominal segment VI and a narrow wing base. The position of *Pityococcus* among Coccoidea is, however, peculiar in our analysis (see discussion section), and a different phylogenetic placement would affect the character mapping. The distribution of Recent *Pityococcus* in the Nearctic region indicates that this genus is a relict taxon that was more widely distributed in the past, with a Palaearctic presence based on the Baltic amber record.

**APTICOCCIDAE, NEW FAMILY**

**Type genus:** *Apticoccus* Koteja and Azar, 2008.

**Diagnosis:** Body minute (less than 800 µm long); head narrow; antennae 10-segmented, with scape almost meeting anteriorly; antennal segments shorter distally, with fleshy
setae on flagellar segments and forming a brush on apical segment; capitate setae absent; ocular sclerite with a row of six simple eyes on each side, ventral eyes located more posteriorly than dorsal eyes and meeting on venter, with a V-shaped appearance; scutellum rectangular and transversly narrow; legs with two finely clavate tarsal digitules, each longer than claw without claw digitules or claw denticles; wings with subcostal and cubital ridges originating at base of wing; surface of wing with microtrichia; hamulohalteres broad, with two hamuli; penial sheath elongate and pointed, at least 1/7th body length.

**Genus included:** *Apticoccus* Koteja and Azar.

*Apticoccus*, Koteja and Azar

**Type species:** *Apticoccus minutus* Koteja and Azar, 2008.

**Occurrence:** Lebanon, Early Cretaceous.

**Diagnosis:** As for family.

**Species included:** *A. minutus, A. fortis* n. sp., *A. longitenuis* n. sp.

*Apticoccus minutus*, Koteja and Azar 2008

**Holotype:** HAM-54A (Cocc-0847) alate male; Dany Azar amber collection, provisionally deposited in the Muséum National d’Histoire Naturelle.

**New material:** 628 (Cocc-1720), alate male in a 3 x 2 x 0.5 mm amber piece embedded in Canada balsam and mounted in epoxy between two coverslips; specimen is in imperfect condition but ventral surface of head is visible, dorsal part covered with a layer of bubbles, antennae well preserved, wings truncate. In the Dany Azar amber collection, provisionally deposited in the Muséum National d’Histoire Naturelle.
**Comments:** Specimen 628 (Cocc-1720) was identified to *Apticoccus minutus* because of the thin and elongate thorax and abdomen, as well as thinner claws, as opposed to *A. fortis* n. sp. and *A. longitenuis* n. sp.. From a further study of the holotype and the addition of new fossil material, the following changes from the original description in Koteja and Azar (2008) are provided: antennae 10-segmented (vs. 9-segmented in Koteja and Azar [2008]; the antennal segments are damaged on the holotype, but segmentation is better preserved on specimen 628), ans each hamulohaltere with two hamuli (vs. “Haltere spindle- shaped, 70 µm long, 20 µm wide, with one seta” Koteja and Azar [2008]; observation of both holotype and specimen 628 show two hamuli).

*Apticoccus fortis*, new species

(Figures 4.12; 4.13)

**Type locality:** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafzet Jabal Loubnon (Central Lebanon).

**Type:** Holotype HAM-1669A, alate male, in a 3 x 2.5 x 0.5 mm yellow transparent rectangular amber piece, embedded in Canada balsam and mounted in epoxy between two coverslips; specimen entire and in good condition with wings spread, but pronouncedly darkened (resembling oxydation) and covered by a thin layer of bubbles; accessible views: ventral and dorsal; In the Dany Azar amber collection, provisionally deposited in the Muséum National d’Histoire Naturelle.

**Etymology:** The epithet is from the Latin nominative “fortis”, meaning “strong” and refers to the more robust body shape compared to *A. minutus* and *A. longitenuis* n. sp.

**Diagnosis:** *Apticoccus fortis* n. sp. differs from other *Apticoccus* spp.by the following characters: head very short, thorax wide, abdomen pear-shaped, tergites wide and tapered
Figure 4.12. Photomicrographs of the new species of *Apticoccus*. A. Dorsal surface of *Apticoccus fortis* n. sp., holotype HAM-1669A, B. Dorsal surface of *Apticoccus longitenuis* n. sp., holotype AD-20, C. Ventral surface of *Apticoccus longitenuis* n. sp. See Materials and Methods section for abbreviations.
Figure 4.13. Details of *Apticoccus fortis* n. sp. A. Antenna, B. Leg, C. Ventral view of penial sheath.
posteriorly, penial sheath round with one pairs of short setae, then abruptly thin and
curved (ca. ⅓ body length).

**Description:** Body minute, total length 545 μm, largest width at mesothorax, 180 μm.

Head: short, difficult to observe, probably partially retracted into prothorax. Simple eyes visible ventrally, forming one row on each side, meeting medially. Probably six pairs of simple eyes (ca. 20 μm wide). Other head structures not observable.

Antenna 10-segmented, with bases of antennae almost meeting anteriorly; total length ca. 220 μm, segments III-X narrower distally; lengths of segments (in μm): scape 20; pedicel 25; III 20-25; IV 25-30; V 25-30; VI 30; VII 30-40; VIII 10-15; IX 15; X 15, each with ca. 5-10 thick setae (ca. 20 μm long), setose and fleshy setae not differentiated. Apical segment with ca. 10 thick setae (probably bristles) forming a brush, each 12-15 μm long.


Wings: forewings elongate with narrow base, round apex; ca. 620 μm long, 260 μm at widest section; subcostal ridge extending from the base to a little less than ¼ of wing length. Cubital ridge present and originating from base, extending posteriorly to about ½ wing length. Alar setae and sensoria absent, minute microtrichia present throughout wing surface. Alar lobes present. Hamulohalteres present, wide, ca. 30 μm long, with two hamuli.
Legs: long, robust, all subequal in length, cuticular reticulations absent; measurements of second pair of legs provided (forelegs not easily measurable); coxa not visible entirely but probably triangular; trochanter and femur 67 µm long, with few, hair-like setae. Tibia length 100 µm, with few short, hair-like setae; tarsus one-segmented, 40 µm long, tarsal spurs undifferentiated, tarsal digitules minutely clavate, longer than claw; claw robust, curved, claw digitule and dентicle not detected.

Abdomen: pear-shaped, 323 µm long (200 µm without genital segment), greatest width 117 µm, tapered gradually apically. Tergites and sternites well developed and segmentation easy to delineate. Abdominal setae, pores and glandular pouches not observable. Genital segment: penial sheath elongate (123 µm), ⅕ of body length, width 30 µm, with one pair of setae of equal length on each side of penial sheath. Aedeagus long and pointed at apex, slightly curved. Eversible endophallus absent.

*Apticoccus longitenuis*, new species

(Figures 4.12B; 4.14)

**Type locality:** Early Cretaceous (Lower Aptian after existing geological maps, but this age is debatable), Ain Dara, Caza Aley (Aley District), Mouhafazit Jabal Libnen (Governorate Mount Lebanon), Central Lebanon.

**Type:** Holotype AD-20, alate male, in a 3 x 2.5 x 0.5 mm yellow, transparent, rectangular amber piece, embedded in Canada balsam and mounted in epoxy between two coverslips; specimen entire and in good condition with wings spread, dorsal surface slightly darkened, ventral surface mostly covered by a large air bubble; accessible views: ventral and dorsal. In the Dany Azar amber collection, provisionally deposited in the Muséum National d’Histoire Naturelle.
Figure 4.14. Details of *Apticoccus longitenuis* n. sp. A. Dorsal view of head and thorax, B. Antenna, C. Leg. D. Ventral view of penial sheath.
**Etymology:** The epithet “longitenuis” comes from the combination of Latin genitive “longi”, meaning “long” and the nominative “tenuis” meaning “thin,” referring to the long, needle-like penial sheath.

**Diagnosis:** *A. longitenuis* differs from other *Apticoccus* species due to the following characters: Head narrow, thorax wide, abdomen wide but abruptly tapering, penial sheath long and needle like, ca. ¼ body length.

**Description:** Body minute, total length 615 µm, widest at mesothorax, 175 µm. Head: short, round, 90 µm long, 50 µm wide; ocular sclerite well developed, with setae, bearing 6 simple eyes of same size (each ca. 15 µm wide), dorsal eyes positioned more anteriorly than ventral eyes, both almost touching dorsally and ventrally. Ocelli present laterally. Dorsal midcranial ridge absent. Ventral midcranial ridge present. Long setae present on both sides of anterior margin of head, between antennae.

Antenna 10-segmented, inserted on anterodorsal side of head, bases almost touching, total length 300-320 µm; measurements for each antennal segment (in µm) scape ca. 20; pedicel 30; flagellar segments III to X all filiform of approximate same length; III 30-35; IV 25; V 35-40; VI 30-40; VII 25-30; VIII 35; IX 30; X 35-40. Setae about same length as segment width (15-20 µm). Apical segment narrower, bearing bristles distally and fleshy setae.

Thorax: head and thorax separated by a slight neck constriction. Prothorax well developed but membranous. Ridges on prothorax not observable. Dorsally: Prescutum oval but pointed anteriorly, without prescutal setae, not obviously separated from scutum; scutum with a medial less sclerotized area extending from prescutum to scutellum;
scutellum rectangular and transversely narrow; mesopostnotum well-developed. All entral meso- and metathoracic structures obscured by a large bubble.

Wings: forewings both well-preserved, oval with narrow base, rounded apex, parallel-sided medially, 715 µm long and 135 µm widest; subcostal ridge extending from base of wing to more than ¾ of wing length. Cubital ridge present, bifurcating at 1/10 of wing length from base, extending to almost same level as subcostal ridge. Alar setae and sensoria absent, microtrichia present throughout wing surface. Alar lobe present.

Hamulohalteres wide, ca. 30 µm long; with two hamuli.

Legs: robust, all of subequal length, cuticular reticulations absent; prothoracic legs: coxa not visible; trochanter and femur, 120 µm long, 30 µm wide, with a few hair-like setae (ca. 10 µm); tibia: 100 µm long, 15 µm wide, with a few hair-like setae, with one differentiated tibial spur; tarsus one-segmented, 40 µm long, tarsal digitules finely clavate, longer than claw; claw short and curved, claw digitule and denticle not detected.

Abdomen: wider at base and tapering gradually posteriad, 380 µm long (210 µm without genital segment), 85 µm widest. Tergites and sternites well developed and segmentation easy to delineate, mostly sclerotized medially. Abdominal setae and pores not visible. Genital segment: penial sheath with a broad anterior capsule, and extremely elongate (170 µm long), ca. 1/4 of total body length, 30 µm wide, anteriorly with three lateral pairs of setae, anterior pair shorter, posterior pairs 4 times longer. Aedeagus needle-like and pointed at apex, not clearly differentiated from penial sheath. Eversible endophallus absent.

Comments: Koteja and Azar (2008) tentatively classified *Apticoccus* in the family Electrococcidae. This family was created by Koteja (2000b) after the author described the
genus *Turonicoccus* from New Jersey amber and suggested that this genus and *Electrococcus* (described from Canada amber [Beardsley, 1969], of Santonian age) belong to the same family. The assignment of *Apticoccus* to Electroccoccidae is, however, uncertain according to Koteja and Azar (2008), probably because of the poorly preserved holotype. Based on newly studied material, we are creating the new family Apticoccidae for *Apticoccus*, based on the following differences with *Turonicoccus* and *Electrococcus*:

- Head small and generally narrower than thorax (vs. head as large as thoracic structures), antennae without short, fleshy setae or capitate setae (vs. capitate setae and presence of short fleshy setae in *Turonicoccus*), apical segments with bristles forming a brush (vs. absent), one tarsal segment (vs. two tarsal segments), scutellum rectangular, tranverse and narrow (vs. enlarged rectangular scutellum), penial sheath spine-like (vs. shorter triangular penial sheath). The phylogenetic analysis retrieved Apticoccidae as a monophyletic family, sister group to a clade including the extinct Albicoccidae from Burmese amber (Koteja, 2004) and the Steingeliidae. Furthermore, *Apticoccus* is not found related to either *Turonicoccus* or *Electrococcus*.

**GENERA INCERTAE SEDIS**

*Priapococcus*, new genus

**Type species:** *Priapococcus creticus* n. sp., by monotypy.

**Occurrence:** Lebanon, Central Lebanon (Hammana). Early Cretaceous.

**Etymology:** The generic *Priapococcus* is composed of *Priapus*, the well-endowed Greek god of reproduction, and *coccus* after the name of the superfamily, referring to the long, penial sheath. Gender: masculine.
**Diagnosis:** Body small but robust, head with two compound eyes bearing 55-60 ommatidia, ocelli found laterally; antennae filiform, almost trinodose, undifferentiated setae on apical segment; ventral ridges forming a five-armed star, narrow on first ½ anterior of head; prescutum oval but horizontally elongate; scutum with an oval membranous area medially, scutellum triangular; forewings with a subcostal ridge, cubital and posterior flexing patch; legs slender, with one-segmented tarsus, tarsal digitules clavate but claw digitule absent; dorsal abdominal segments VII and VIII with each a row of 10 tubular ducts; penial sheath extremely elongate.

**Priapococcus creticus,** new species

(Figures 4.15; 4.16)

**Type locality:** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnon (Central Lebanon).

**Type:** Holotype 1215, alate male, in a 6.5 x 5 x 0.5 yellow, transparent, polished amber piece, embedded in Canada balsam and mounted in epoxy between two coverslips; specimen very well preserved with both wings spread, abdomen obstructed by a large air bubble. In the Dany Azar amber collection, provisionally deposited in the Muséum National d’Histoire Naturelle.

**Etymology:** The epithet derives from the Latin from “creta”, meaning “chalk” and refers to the Cretaceous Period.

**Diagnosis:** As for genus.

**Description:** Body small but robust, 1.44 mm long total, largest width at mesothorax, 328 µm. Head: transverse, dorsoventrally flattened, 300 µm wide, 100 µm long. Ocular sclerite with a pair of compound eyes protruding laterally, eye length 85-95 µm, each
Figure 4.15. Photomicrographs of *Priapococcus* n. gen. A. Dorsal surface of *Priapococcus creticus* n. sp. holotype 1215, B. Ventral surface of holotype 1215. See Material and Methods for abbreviations.
Figure 4.16. Details of *Priapococcus creticus* n. sp. A. Dorsal view of head, B. Dorsal view of mesothorax, C. Ventral view of pro- and mesothorax, D. Antenna, E. Leg, F. Penial sheath.
with about 55-60 ommatidia. Ocelli present posterior to compound eyes, 18 µm wide. Dorsal midcranial ridge well-developed and probably extending to a postoccipital ridge. Ventral surface of head with ridges forming a five-armed star, comprising the midcranial ridge, starting on anterior margin and fusing with two preocular ridges and two preoral ridges. Ridges concentrated on anterior part of head.

Antenna 10-segmented and long, total length 960-1000 µm; lengths of segments (in µm): scape 30-40; pedicel 35-40; flagellar segments III to X all filiform, almost trinodose; III 75-82; IV 120-125; V 120-130; VI 125-135; VII 120-125; VIII 105-110; IX 105-110; X 110-115. All flagellar segments covered with two sizes of setae: long hair-like setae (40-60 µm) and short hair-like setae (25 µm), randomly distributed. Apical segment without bristles or capitate setae.

Thorax: head and thorax separated by a slight neck constriction. Prothorax well-developed and membranous. Ridges on prothorax not observable dorsally; ventrally, prosternum with a median ridge extending to basisternum. Mesothorax dorsally: Prescutum suboval, transversely elongate (ca. 150 µm wide, 50 µm long), with prescutal setae; scutum with an oval membranous area medially, adjacent to prescutum but not touching scutellum, scutal setae present; scutellum triangular (ca. 160 µm wide, 70 µm long), with two lateral areas. Mesosternum short (45 µm long).

Wings: forewing suboval, narrow at base but widening rapidly, almost parallel-sided medially and rounded distally, 1135-1145 µm long and 460-465 µm at widest section; subcostal ridge extending from base of wing to more than ⅔ wing length. Cubital ridge starting at 270 µm from wing base and fading to wing midlength; posterior flexing
patch beginning at almost same location aspr cubital ridge. Alar setae, microtrichia and alar sensoria absent. Alar fold present. Hamulohaltere not visible.

Legs: long and robust, cuticular reticulations absent; prolegs: coxa 60 µm long; trochanter and femur, 38 µm wide, 150 µm long on proleg, with a few hair-like setae; tibia: 170 long µm, 25 µm wide, with hair-like setae becoming spine-like ventrally; tarsus one segmented, 85 µm long, 16 µm wide; tarsal digitules narrowly clavate; claw narrow, 20 µm long, almost straight, claw digitules and denticles absent.

Abdomen: cylindrical, ca. 995 µm long (433 µm without penial sheath), 300 µm widest, progressively tapering posteriorly from segment VI. Tergites and sternites well-developed and segmentation easy to delineate; without caudal extensions on abdominal segments. Tergite VII and VIII with each, one row of ca. 10 tubular ducts, extruding wax filaments. Genital segment: penial sheath elongate with a thick pointed apex, 560 µm long, 74 µm wide at base, becoming narrow and parallel-sided at 125 µm from penial sheath base. Aedeagus slender and pointed at apex. Eversible endophallus not visible.

**Comments:** Although all general structures of *Priapococcus* indicate a close relationship to Xylococcidae and related families, this genus has a peculiar combination of characters. The presence of a membranous area medially on the scutum is found in the Coelostomidiidae and Monophlebidae, and the two lateral areas on the corners of the rectangular scutellum is characteristic of the Recent Callipappidae, Coelostomidiidae and Monophlebidae (but also found in extinct Grohniidae, which was dsccribed as a xylococcid-like family). *Priapococcus* cannot be assigned to either of these families due, for instance, tothe differences in antennal structure (very short antennal setae in *Callipappus*, and binodose or trinodose segments in Monophlebidae), the very narrow
posterior margin of basisternum, and the multiple claw digitules in Coelostomidiidae.

Table 4.2. suggests a relationship with Grohniidae, although the tarsal digitules in *Priapococcus* are clavate. Finally, the elongate and spine-like penial sheath of *Priapococcus* is peculiar for any taxa related to Xylococcidae. The other genera with compound eyes and bearing this type of penial sheath are *Kozarococcus* n. gen. and *Alacupacoccus* n. gen.. Finally, the morphological analysis does not allow any conclusions on the sister group to *Priapococcus*, although it was retrieved within a clade including Xylococcidae, all xylococcid-like families, Kozarococcidae n. fam., Lebanonococcidae and *Alacupacoccus* n. gen. (described below). For now and until further study, we consider *Priapococcus* as incertae sedis.

*Alacupacoccus*, new genus

**Type species:** *Alacupacoccus peculiaris* n. sp., by monotypy.

**Occurrence:** Myanmar: Kachin: near Tanai village. Albian-Cenomanian boundary.

**Etymology:** The genus name comes from the Latin “ala”, meaning “wing”, “cupa”, meaning “notched”, and “coccus” for coccoid. This refers to the notch found on the apex of the forewing. Gender masculine.

**Diagnosis:** Body minute, head large, compound eyes bulging, each with fewer than 100 ommatidia; antennae segments filiform, with capitate and fleshy setae on apical segment; wings hyaline, with a subcostal ridge extending to ¾ wing length, cubital ridge present ending at apical margin with a notch; hamulohalteres long and narrow; legs slender, tarsus one-segmented, tarsal digitule capitate; claws narrow and elongate almost straight,
claw digitules and denticles absent; tubular duct on abdominal tergites absent; genital segment exceptionally elongate.

**Species included:** *A. peculiaris* n. sp.

*Alacupacoccus peculiaris*, new species

(Figures 4.17; 4.18)

**Type locality:** Myanmar: Kachin: near Tanai village. Albian-Cenomanian boundary.

**Type:** Holotype AMNH Bu-1516, alate male in a 5 x 4 x 0.5 mm dark yellow transparent, polished amber piece, specimen lying on a resin layer, thoracic and abdominal regions not well preserved, only one wing spread; accessible views: ventral and dorsal. Myanmar, Kachin, Tanai Village, on Ledo Road, 105 km NW Myitkyna), Leeward Capitol Corp coll., deposited in American Museum of Natural History.

**Etymology:** The epithet is from the Latin ”peculiaris” and refers to the peculiarity of the notch on the wing, unique to all Coccoidea..

**Diagnosis:** Same as for genus.

**Description:** Body minute, total length 990 µm, largest width at mesothorax 200 µm. Head: transverse, 180 µm wide, 90 µm long. Ocular sclerite a pair of large compound eyes protruding laterally, 75 µm long, number of ommatidia difficult to determine but probably ca. 100. Ocelli bulging laterally, posterior to compound eyes, as in *Matsucoccus*. No head structure visible.

Antenna 10-segmented and long, total length ca. 450 µm; measurements for each antennal segment (in µm): scape 35; pedicel 50; flagellar segments III to X all filiform; III 65; IV 55; V 45; VI 55; VII 45; VIII 30; IX 700. All flagellar segment covered
Figure 4.17. Photomicrograph of *Alacupacoccus peculiaris* n. sp., dorsal surface of holotype AMNH Bu-1516. See Material and Methods for abbreviations.
Figure 4.18. Details of *Alacupacoccus peculiaris* n. sp. A. Dorsal view of head, B. Antenna, C. Leg from femur, D. Forewing.
With 10-15 long hair-like setae (each 25-30 µm). Apical segment with hair-like setae, two capitate setae and at least one bristle.

**Thorax:** head and thorax separated by a neck constriction. All thoracic structures damaged, and not identifiable.

**Wings:** forewings broad at base, rounded at apex, with a notch on termen, 680 µm long, 330 µm wide; subcostal ridge extending from the base of the wing to more than \( \frac{3}{4} \) wing length. Cubital ridge starting at 130 µm from wing base, extending diagonally to tip of wing, ending at wing notch. Alar setae and sensoria absent, microtrichia absent. Alar fold present. Hamulohalteres elongate and narrow, 50 µm long, each with two hamuli.

**Legs:** long and slender, all of subequal length, cuticular reticulations absent; prothoracic legs: coxa 72 µm long; trochanter and femur, 20 µm wide, 195 µm long, with numerous thick hair-like setae of same length as femur width; tibia: 155 µm long, 17 µm wide, with hair-like setae, tibial spurs not differentiated; tarsus one-segmented, 60 µm long, 17 µm wide, tarsal digitules narrowly clavate; claw narrow, 30 µm long, almost straight, claw digitules and denticles absent.

**Abdomen:** short, probably retracted, tapering posteriorly, ca 635 µm long (183 µm without penial sheath), 125 µm widest. Abdominal setae visible on last two abdominal segments. Genital segment: penial sheath elongate with a pointed apex, 460 µm long, 35 µm wide at base, becoming narrow and parallel-sided (20 µm wide) 60 µm from penial sheath base. Aedeagus slender and pointed at apex. Eversible endophallus absent.

**Comments:** *Alacupacoccus* seems most similar to *Kozarococcus* because of the minute body size, head shape, bulging compound eyes, and the elongate penial sheath. However,
they differ by the wing structure (*Alacupacoccus* has a notch on the apex of the forewing, which is also unique in Coccoidea) and the absence of tubular ducts.

The phylogenetic results retrieved *Alacupacoccus* as sister group to *Lebanococcus* and together are defined by wings with a subcostal and cubital ridges only and without tubular ducts. Despite the presence of well-developed compound eyes, *Lebanococcus*, has a very different, telescopic abdomen (Koteja and Azar, 2008), and shortened antennae. Although the phylogenetic results suggest that *Alacupacoccus* is in the same family as *Lebanococcus* (i.e., the Lebanococcidae), the diagnostic features of the family do not fit the characters found in *Alacupacoccus*. In our analysis, *Alacupacoccus* + *Lebanococcus* were found to be the sister group to the Kozarococcidae, but the phylogenetic placement of *Alacupacoccus* needs to be further investigated with additional, better preserved specimens (the unique specimen has all thoracic structures damaged). For now, the genus is considered as family *incertae sedis*.

**Magnaelentis**, new genus

**Type species:** *Magnaelentis glaesaria* n. sp., by monotypy.

**Occurrence:** Myanmar: Kachin: near Tanai village. Albian-Cenomanian boundary.

**Etymology:** The genus name comes from the Greek “exo”, for “bulging” and “omma” for “eye” in reference to the large protruding eyes. Gender: feminine.

**Diagnosis:** Body large, head with ocular sclerites each bearing eight pairs of large and bulging simple eyes; antennae filiform, almost trinodose, with long setae; forewings with microtrichia; legs slender, tibia with setae becoming spine-like on ventral surface distally; tarsus two-segmented; claw with spine-like digitules; abdominal segment VIII
with a pair of wax filaments, indicative of a pair of glandular pouches. Penial sheath large triangular, with a narrow aedeagus.

**Species included:** *M. glaesaria* n. sp.

*Magnaelentis glaesaria*, new species.

(Figures 4.19; 4.20)

**Type locality:** Myanmar, Kachin: near Tanai Village. Albian-Cenomanian boundary.

**Type:** Holotype AMNH Bu-1418, alate male in a 4 x 7 x 1.5 mm rectangular, yellow, transparent polished amber piece with a large crack passing through the specimen; specimen well preserved but only lateral views observable. Myanmar, Kachin, Tanai Village, on Ledo Road, 105 km NW Myitkyna), Leeward Capitol Corp coll., deposition American Museum of Natural History.

**Etymology:** The epithet is the Latin “glaesarius”, meaning “of amber”.

**Diagnosis:** Same as for genus.

**Description:** Body small, total length 1.37 mm long, widest width not measurable. Head: frontally flat ca. 290 µm wide, 140 µm long. Head structures not visible except for an ocular sclerites which surrounds head, each bearing seven pairs of large, protruding simple eyes.

Antenna: 10-segmented, total length 950 µm; segment lengths (in µm): scape ca. 45 µm long; pedicel, 80 µm long, with several groups whorls of long setae (ca. 65 µm); segments III-X all filiform: III 93; IV 122; V 100; VI 95; VII 115; VIII 100; IX 100; X 100. Antennal setae longer than segment width (55-65 µm long). Differentiated setae on apical segment not observed.
Figure 4.19. Photomicrographs of *Magnaelentis glaesaria* n. sp. lateral view of holotype AMNH Bu-1418. See Material and Methods for abbreviations.
Figure 4.20. Details of *Magna lentis glaesaria* n. sp. A. Head from lateral side, B. Antenna, C. Leg, D. Penial sheath from lateral side.

Wings: forewings well-developed, round with broad base and a rounded apex; 1.28 mm long, 640 µm wide; subcostal ridge extending from base of wing to more than ¼ wing length. Cubital ridge 200 µm from wing base, extending to same level as subcostal ridge. Posterior flexing patch present. Wing covered with microtrichia; alar setae present, sensoria not observed. Anal lobe present. Hamulohalteres broad, each with two hamuli.

Legs: long and slender, all of subequal length; prothoracic leg: coxa triangular, 70 µm long; trochanter and femur fused, ca 300 µm long, 30 µm wide on prolegs; tibia: 280 µm long, 28 µm wide, tarsus two-segmented, 160 µm long, and 20 µm wide, tarsal digitules; claw narrow almost straight, 30 µm long, claw digitule spine-like, claw denticle absent.

Abdomen cylindrical, 700 µm long (440 µm without genital segment). Setae are visible but frequency and distribution uncertain. Abdominal segment VIII with a pair of glandular pouch laterally, each extruding two long wax filaments. Genital segment: penial sheath elongate triangular, about 245 µm long, with a few setae anteriorly. Aedeagus narrow, almost as long as penial sheath, pointed.

Comments: *Magnaelentis* definitely belongs to the taxa bearing a row multiple simple eyes. This genus seems most similar to *Puto* by the following characters: the long antennal setae, the tarsus is two-segmented, with similar tibial spurs, with presumably glandular pouches on abdominal segment VIII, each with two wax filaments, and the subtriangular, elongate penial sheath with a narrow aedeagus. However, significant
differences also occur: the ocular sclerite bear very large and protruding eyes (vs. small eyes), hamulohalteres bear two hamuli (vs. four hamuli), the tarsal digitules are undifferetiated (vs differentiated), the claw denticles are absent (vs. present). The phylogenetic results based on morphological characters retrieved Magnaelentis as sister genus of Solicoccus (Labiococcidae) described in New Jersey amber (Koteja, 2000).

Solicoccus differs from Magnaelentis by the small size and diagonal arrangement of simple eyes in the former, the presence of glandular pouches on abdominal segments VII and VIII (vs. only on segment VIII in Magnaelentis), and three hamuli on the hamulohaltere (vs. two). Unfortunately, the specimen orientation does not allow a comparison of the thoracic structures, and before more specimens are found, Magnaelentis is considered as an incertae sedis.

Pedicelloccocus, new genus

Type species: Pedicelloccocus marginatus n.sp., by monotypy.


Etymology: The genus name Pedicelloccocus is from the Latin pedicellus, diminutive of pes, “foot, or pedicel” and, refers to the enlarged and bulbous pedicel of this new genus. [Diagnosis: Body minute, head round and large relatively to body size, ocular sclerites each with apparently five or six pairs of simple eyes, ventral eyes larger than lateral eyes, not meeting medi ally; antenna 9-segmented with an exceptionally enlarged pedicel, heavily reticulated and with many short spinose setae; flagellar segments irregular in shape, apical segment narrower; prescutum round, scutellum suboval; mesopostnotum almost as long as scutellum; basisternum with a median ridge; forewings with a narrow base and distally flat; hamulohalteres each with two hamuli; legs small; abdomen
parallel-sided, tapering from segment VI; penial sheath of *Pityococcus*-type; eversible endophallus present.

**Species included:** *P. marginatus* n. sp.

*Pedicellocccus marginatus*, new species

(Figures 4.21, 4.22)

**Type locality:** Myanmar: Kachin: near Tanai Village. Albian-Cenomanian boundary.

**Type:** Holotype AMNH-BU458 alate male; Myanmar, Kachin, Tanai Village, on Ledo Road, 105 km NW Myitkyna), Leeward Capitol Corp coll., deposited in American Museum of Natural History.

**Etymology:** The epithet is from the Latin “marginatus”, meaning “marginated”, and refers to the flat apical margin of the wing.

**Diagnosis:** As for genus.

**Description:** Body minute, total length 520 µm, largest width at mesothorax, 165 µm.

Head: subrotund, 135 µm wide. Ocular sclerites well developed, each with at least 5 pairs of simple eyes (probably 6 but most dorsal eye not visible because of specimen orientation). Ocelli not observed on specimen but probably present.

Antenna 9-segmented, each with an extremely enlarged pedicel; total length 195-200 µm; lengths of segments (in µm) scape ca. 20; pedicel 55-60 long, with reticulations and numerous short spinose setae; segments III to IX ca. 20, with hair-like setae. Apical segment slightly narrower, with 4 capitate setae and 2 large, curved bristles.

Thorax: head and thorax separated by a slight neck constriction. Prothorax membranous. Ridges on prothorax not visible. Mesothorax dorsally: Prescutum suboval,
Figure 4.21. Photomicrograph of *Pedicelloccus marginatus*, n. sp. A. Dorsal side of holotype AMNH Bu-458, B. Ventral side of holotype AMNH Bu-458. See Materials and Methods for abbreviations.
Figure 4.22. Details of *Pedicelloccus marginatus* n. sp. A. Ventral view of head, B. Dorsal view of mesothorax, C. Wing, D. Foreleg, E. Posterior abdominal and genital segments.
scutum hidden by wings, scutellum suboval (rounded anterior margin) with an apparent median ridge, ca. 40 µm long, 50 µm wide; mesopostnotum slightly longer than scutellum. Ventrally: basisternum 55 µm long, 100 µm wide, with a basisternal median ridge; setae not observed.

Wings: forewings very broad and rounded distally, base narrow, apical margin almost flat; ca. 500 µm long, 280 µm at widest section; subcostal ridge extending from base to more than ¾ wing length. Cubital ridge present, point of origin unclear. Alar setae and sensoria absent, minute microtrichia present throughout wing surface. Alar lobe present. Hamulohalteres present, hamuli not detected.

Legs: small, of subequal length, cuticular reticulations absent; prothoracic legs: coxa not visible; trochanter and femur, ca. 90 µm long, ca.18 µm wide, with hair-like setae; tibia: 80 µm long, 20 µm wide, setae not visible; tarsus one-segmented, 40 µm long, 10 µm wide, setae not visible; claw small, digitules and denticles not observable.

Abdomen: elongate and narrow, almost parallel-sided, tapering slightly distally (ca. 80 µm widest), 240 µm long (without genital segment ca. 195 µm). Segmentation easy to delineate. Abdominal pores not visible, pleural abdominal setae present pleurally, with a pair of longer setae on segment VIII, glandular pouches not detected. Genital segment: penial sheath triangular, of Pityococcus-type (45 µm long, 22 µm wide at base), bifurcated apically. Aedeagus about same length as penial sheath. Eversible endophallus present.

Comments: Pedicellococccus n.gen. is similar to Pityococcus by having a tapered abdomen, ending with a triangular, apically blunt and bifurcate penial sheath, with an endophallus. However, the antennal segments (with absence of blunt, short, fleshy setae
in *Pedicelloccocus*, head structures (eye rows arranged diagonally in *Pityococcus*, horizontally in *Pedicelloccocus*), and wing shape (apically flat in *Pedicelloccocus*) all differ, including the extremely small size of *Pedicelloccocus*. The pedicel is extremely enlarged, which is only known in *Turonicoccus*, described in New Jersey amber (Koteja, 2000b). However, *Turonicoccus* has antennal segments that are more nodose, which resemble *Pityococcus*. The phylogenetic analysis retrieved *Pedicelloccocus* as sister genus to *Pityococcus*, and these together being the sister group to *Turonicoccus*.

*Turonicoccus* had been assigned to the Electrococcidae (Koteja, 2000b) but they have not been found to closely related in our analysis. If *Turonicoccus* and *Pedicelloccocus* were considered as Pityococcidae, the morphological variation of this family would be expanded. Thus far, we consider *Pedicelloccocus* as a genus *incertae sedis*. It is amongst the smallest Coccoidea found in Burmese amber.

FAMILY PSEUDOCOCCIDAE HAYMONS

*Eopseudococcus*, new genus

**Type species:** *Eopseudococcus megalops* n. sp., by monotypy.

**Occurrence:** Lebanon, Central Lebanon, Hammana. Early Cretaceous.

**Etymology:** The genus names is the combination of the Greek “eos”, meaning “dawn, early” and “pseudococcus” in reference to the family Pseudococcidae. This name refers to the early occurrence of a member of this family in Lebanese amber.

**Diagnosis:** Body minute, head not distinctively separated from prothorax, each ocular sclerite with a dorsal and a ventral simples eye; ventral eyes meeting medially and larger than dorsal eyes; antennae with setae longer than segment width; basisternum with a median ridge; forewings elongate and thin with microtrichia; hamoluhalteres long and
thin, with one long hamulus; legs slender, each with one tibial spur; tarsus two-
segmented, tarsal digitule thinly clavate; claw digitules and denticles absent; abdominal
segments VII and VIII with wax filaments, indicative of glandular pouches; penial sheath
short.

Species included: E. megalops n. sp.

Eopseudococcus megalops, new species

(Figures 4.23A,B; 4.24)

Type locality: Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafzet Jabal
Loubnon (Central Lebanon).

Type: Holotype 1582, alate male in a 4 x 4 x 0.5 mm yellow, transparent, polished amber
piece, embedded in Canada balsam and mounted in epoxy with two coverslips, with a
few particles of debris; specimen is well preserved, although the wings are hardly visible
and antennae truncated. accessible views: ventral and dorsal. In the Dany Azar amber
collection, provisionally deposited in the Muséum National d’Histoire Naturelle.

Etymology: The epithet megalops comes from Greek megalo, meaning “large or great”
and ops, (f) “eyes”, referring to the large ventral eyes, on this species.

Diagnosis: As for genus.

Description: Body minute, total length 775 µm, widest at mesothorax, ca. 235 µm. Head:
round ventrally, protruding, ca. 210 µm wide, ca. 170 µm long. Each ocular sclerites with
a twi pairs of simple eyes (a pair dorsally and a pair ventrally), each dorsal eye ca. 25 µm,
ventral eye larger than dorsal eye (ca. 40 µm) and positioned closer together; with a pair
of lateral ocelli (10 µm wide).
Figure 4.23. Photomicrographs of *Eopseudococcus* n. gen. and *Geropseudococcus* n. gen. A. Dorsal surface of *Eopseudococcus megalops* n. sp. holotype 1582, B. Ventral surface of holotype 1582, C. Dorsal surface of *Geropseudococcus eukrinops* n. sp. holotype AMNH Bu-1594, D. Ventral surface of holotype AMNH Bu-1594. See Materials and Methods for abbreviations.
Figure 4.24. Details of *Eopseudococcus megalops* n. sp. A. Dorsal view of head, B. Ventral view of head, C. Dorsal mesothorax, D. Wing, E. Connection of the forewing and hamulohaltere, F. Leg.
Antenna: at least 6-segmented, but both antennae broken on holotype; lengths of segments (in µm): scape 25; pedicel 40; flagellar segments III to VI all filiform, subequal in length (ca 100 µm). Setae longer than segment width (ca. 35-60 µm).

Thorax: head and thorax slightly separated. Prothorax membranous, ridges not observable. Prosternal structure not visible. Mesothorax dorsally: with an oval bulging prescutum (85 µm wide, 72 µm long); scutum without a membranous area; scutellum oval almost as wide as prescutum. Setae not detected. Ventrally: basisternum well developed with a median ridge.

Wings: forewings elongate and thin, base narrow and round distally, ca. 885 µm long, 290 µm wide; subcostal ridge extending from the base of the wing to a little less than ¾ wing length. Cubital ridge present, starting at wing base; alar setae and sensoria absent, microtrichia present. Alar lobe present. Hamulohalteres narrow, ca. 70 µm long; each with one hamulus.

Legs: long and slender, all subequal in length and shape, cuticular reticulations absent; measurements of foreleg: coxa 50 µm long; trochanter and femur, 150-160 µm long, 25-30 µm wide, with few short, hair-like setae; tibia: 130-160 µm long, 20 µm wide, with short hair-like setae, becoming numerous and spinose distally; tarsus two-segmented, 45-50 µm long, 15 µm wide, tarsal digitules finely clavate; claw thin 10 µm, almost straight, digitules and denticles not observed.

Abdomen: ca. 345 µm long (315 µm without genital segment), 215 µm widest. Tergites and sternites well developed and segmentation easy to delineate. Abdominal setae not visible except for pleural setae on posteriormost segments. Tergite VII and VIII each side having wax filaments protruding out posteriad, indicating glandular pouches.
Genital segment: penial sheath short subtubular (40 µm long, 50 µm at base). Aedeagus not visible. Eversible endophallus absent.

**Comments:** *Eopseudococcus* is a neococcoid genus (it possesses two pairs of simple eyes) and was classified in the Pseudococcidae because of the presence of wax filaments extending from the lateral sides of abdominal segments VII and VIII, indicative of the presence of glandular pouches. Glandular pouches on both abdominal segments are found in the Phenacoccinae (Pseudococcidae), such as in *Ceroputo* (Afifi, 1968) and *Phenacoccus*. However, the wing shape and relative size of the ventral and dorsal eyes differ from *Ceroputo*; *Eopseudococcus* has a very narrow wing and has very large ventral eyes. *Eopseudococcus* also differs from *Geropseudococcus* n.gen., described as new below, by the latter having the dorsal and ventral eyes subequal in size and not meeting medially; the wing is particularly narrow in *Eopseudococcus* but round in *Geropseudococcus*; the penial sheath is longer and the antennal setae are short in *Geropseudococcus*. However, the phylogenetic analysis failed to retrieve *Eopseudococcus* as included within or related to the family Pseudococcidae (as well as any relationship with *Ceroputo*, which was sampled in the analysis), although *Eopseudococcus* is clearly subordinate within the neococcoids. This is probably due to the large amount of missing data for this taxon, so further character coding is required to resolve the relationships of this genus. For now we consider *Eopseudococcus* Pseudococcidae, and as such it is the oldest known fossil mealybug.
**Geropseudococcus**, new genus

**Type species:** *Geropseudococcus eukrinops* n. sp., by monotypy.

**Etymology:** The genus name comes from the Greek “geras”, meaning “old age”, and “pseudococcus” for the family Pseudococcidae.

**Occurrence:** Myanmar: Kachin: near Tanai village. Albian-Cenomanian boundary.

**Diagnosis:** Body minute; head round, separated from thorax by a neck constriction, with two pairs of simple eyes of same size, both sides not joining medially; Antenna 10 segmented with setae shorter than segment width; basisternum without a median ridge; wings oval, hamulohalteres not visible; legs slender, tarsus one segment, tarsal digitule, claw digitule and denticle absent; abdominal segments VII and VIII with wax filaments protruding posterioly, indicating glandular pouches; penial sheath subtriangular.

**Species included:** *G. eukrinops* n. sp.

**Geropseudococcus eukrinops**, new species

(Figures 4.23C-D; 4.25)

**Type locality:** Myanmar: Kachin: near Tanai Village. Albian-Cenomanian boundary.

**Type:** Holotype AMNH Bu-1594, alate male in a 3 x 4 x 1 yellow, transparent, polished amber piece with somedebris; specimen is in good condition, but tilted and bent, the wings spread but hardly visible; accessible views are the ventral and dorsal surfaces of the abdomen and dorsum of the head. Myanmar, Kachin, Tanai Village, on Ledo Road, 105 km NW Myitkyna), Leeward Capitol Corp coll., deposited in American Museum of Natural History.

**Etymology:** The epithet comes from the Greek “eukrines”, meaning “well-separated”, referring to the ventral eyes being far apart from each other.
Figure 4.25. Details of *Geropseudococcus eukrinops* n. sp. A. Ventral view of head, B. Antenna, C. Leg, D. Dorsal view of penial sheath.
Description: Body small but robust, 840 µm long (body bent, true length probably nearer 900 µm), widest at mesothorax (ca. 300 µm wide). Head: round, ventrally protruding, ca 210 µm wide, ca. 170 µm long. Ocular sclerites without setae, each with a dorsal and ventral simple eye; both dorsal and ventral eyes 30 µm wide, not meeting medially; with a pair of lateral ocelli (10 µm wide). Ventral or dorsal midcranial ridge not observed.

Antenna 10-segmented, total length 510-530 µm; lengths of each segment (in µm): scape 40-50; pedicel 60-73; flagellar segments III to X all filiform, subequal in length; III 60; IV 45; V 50; VI 55; VII 60; VIII 45; IX 40; X55. Hair-like setae shorter than segment width (setae ca. 20 µm long). Segment X with one short bristle and 4 longer flagellate setae.

Thorax: head and thorax separated by a neck constriction. Prothorax membranous, ridges not observable. Prosternal structure not visible because of orientation of specimen. Mesothorax dorsally: prealare well developed; with an oval bulging prescutum (100 µm wide, 90 µm long); scutum without a membranous area; scutellum oval, almost as wide as scutum. Setae not detected. Ventrally: basisternum well developed, without a median ridge.

Wings: forewings of neococcoid type, base narrow and rounded distally, ca. 800 µm long, 400 µm wide; subcostal ridge extending from base of wing to a little more than ¾ wing length. Cubital ridge present, starting at wing base; alar setae and sensoria absent, microtrichia present. Alar lobe present. Hamulohalteres narrow, ca. 30 µm long; each with one hamulus.

Legs: long and slender, all subequal in length and shape, cuticular reticulations absent; foreleg: coxa 50 µm long; trochanter and femur, 210 µm long, 28 µm wide, with
few, short hair-like setae; tibia: 155 µm long, 22 µm wide, with short hair-like setae, becoming more numerous and spinose distally; tarsus one-segmented, 80 µm long and 20 µm wide, tarsal digitules undifferentiated; claw narrow, 10 µm long, almost straight; digitules and denticles not identified.

Abdomen: ca. 500 µm long, 210 µm widest (length without genital segment ca. 415 µm). Tergites and sternites well developed and segmentation easy to delineate. Abdominal setae not visible except for pleural setae on posterior most segments. Tergite VII and VIII each with a pair of long setae on each side. Genital segment: penial sheath subtriangular (130 µm long, 65 µm at base). Aedeagus slender and pointed at the apex. Eversible endophallus absent.

**Comments:** As in *Eopseudococcus* n. gen., *Geropseudococcus* n. gen., with its two pairs of simple eyes and wax filaments protruding laterally from abdominal segments VII and VIII, is classified in the Pseudococcidae and probably close to Phenacoccinae. This genus has very short antennal setae, which is peculiar for the family. For comparison with *Eopseudococcus*, see comments section of *Eopseudococcus*. The phylogenetic analysis was also unconclusive as to the relationship of *Geropseudococcus* but was retrieved as belonging to the neococcoids.

**FAMILY COCCIDAE FALLEN**

*Rosahendersona*, new genus

**Type species:** *Rosahendersona prisca* n. sp., by monotypy.

**Occurrence:** Myanmar: Kachin: near Tanai village. Albian-Cenomanian boundary.
Etymology: The genus name is in tribute to Rosa C. Henderson, who has provided major contributions to the study of the fascinating scale insect fauna of New Zealand. Gender: feminine.

Diagnosis: Body minute; antennae filiform, with capitate setae on apical segment; head with ocular sclerite bearing two pairs of simple eyes, dorsal eyes located anterolaterally, ventral eyes almost meeting posteriorly; ocelli present laterally; prescutum rectangular; scutum with a square membranous area medially, scutellum rectangular; basisternum without median ridge; hamulohalteres absent; penial sheath short and wide, parallel-sided and apically tapered.

Species included: *R. prisca* n. sp.

*Rosahendersona prisca*, new species

(Figures 4.26; 4.27)

Type locality: Myanmar: Kachin: near Tanai Village. Albian-Cenomanian boundary.

Type: Holotype AMNH Bu-835, alate male in a 7 x 5 x 1 mm yellow, transparent polished amber piece; specimen in good condition with wings spread but hardly visible; accessible views are ventral and dorsal. Myanmar, Kachin, Tanai Village, on Ledo Road, 105 km NW Myitkyna), Leeward Capitol Corp coll., deposited in American Museum of Natural History.

Etymology: The epithet “prisca” is the feminine of Latin “priscus” meaning “ancient”, a reference to a Cretaceous member of the Coccidae.

Diagnosis: As for genus.

Description: Body minute, total length 535 µm, largest width at mesothorax 180 µm.

Head square-shaped, 100 µm wide, 90 µm long. Dorsal head ridges (if present) obscured
Figure 4.26. Photomicrograph of the holotype of *Rosahendersona prisca* n. sp.  
A. Dorsal surface, B. Ventral surface. See Materials and Methods for abbreviations.
Figure 4.27. Details of *Rosahendersona prisca* n. sp. A. Ventral view of head, B. Dorsal view of mesothorax, C. Ventral pro- and mesothorax, D. Antenna, E. Leg from femur, F. Ventral view of abdominal segments VII and VIII and penial sheath.
by an air bubble. Ventral midcranial ridge short, not extending to ventral eyes. Ocular sclerite without setae, with two pairs of simple eyes, of same diameter (23 µm), ventral eyes meeting medially, dorsal eyes situated anteriorly and almost laterally; ocelli present laterally (9 µm wide), posterior to dorsal eyes. Genae present, without setae.

Antenna 10-segmented, total length 325-350 µm; measurements for each segment (in µm): scape: 20-25; pedicel: 45-50; III: 40-45; IV: 35-40; V: 35; VI: 35-40; VII: 30-35; VIII: 25-30; IX: 25-30; X: 28. All segments bearing hair-like setae but flagellar segments (III to X) also bearing additional fleshy setae. All flagellar segments with hair-like setae as long as width of antennal segment (ca. 15 µm), but also with a pair of longer, hair-like setae (ca. 30 µm) on segments II-X. Apical segment with four long, capitate setae, two bristles, and 3-4 fleshy setae of same length as other shorter setae on flagellar segments.

Thorax: head and thorax separated by a distinct, narrow neck constriction. Prothorax membranous, but no ridges visible. Dorsally: prescutum rectangular and horizontally broad (75 µm wide, 45 µm long); scutum with square membranous area medially; scutellum rectangular (60 µm wide, 30 µm long). Mesopostnotum well developed (50 µm long). Ventrally: basisternum without a median ridge, 107 µm wide, 70 µm long; anterior part of basisternum subequal to posterior part, lateropleurite well developed.

Wings: forewings of neococcoid type, ca. 605 µm long, narrow at base, rounded distally, subcostal ridge short, extending to less than ¾ total wing length, with microtrichia. Alar setae and sensoria absent. Hamulohaltere absent.

Legs: long and slender; coxa triangular, 45 µm long on procoxa; trochanter and femur 23 µm wide, 110-120 µm long on prolegs. Protibia: 100-110 µm long and 17 µm
wide, with hair-like setae at least as long as tibial width, with a differentiated tibial spur, tarsus one-segmented, 35-40 µm long, 10 µm wide, tarsal digitules finely clavate, reaching level of tip of claw; claw thin, almost uncurved, 20 µm long, claw digitules finely clavate, shorter than tarsal digitules, claw denticle absent.

Abdomen: relatively wide, parallel-sided, 230 µm long, 110 µm widest, pleural setae present, with 3 or 4 longer setae on segment VIII, probably where glandular pouches are located. Genital segment: penial sheath subquadrate, short, with anterior half parallel-sided, pointed apically, 72 µm long, 40 µm wide at base. Aedeagus thin and pointed.

Comments: This new genus is a definitive member of the family Coccidae based on the following combination of characters: two pairs of simple eyes, absence of hamulohalteres, presence of a square medial membranous area on the scutum, a rectangular scutellum, and a narrow neck constriction separating the head and thorax. The morphological phylogenetic analysis retrieved *Rosahendersona* within the Coccidae and sister to *Ceroplastes*. However, when looking at character changes, most of the characters supporting the family are either females characters or male characters that are not visible in the fossils (thus coded as missing). In comparing this taxon to the Recent genera of Coccidae, the following combinations of characters did not allow attribution to any extant genus where adult males are known: number of eyes, absence of basisternal median ridge, absence of hamulohalteres, and the presence of ocelli. Additionally, the penial sheath is particularly short compared to extant Coccidae. This species is the first definitive occurrence of Coccidae in the Cretaceous and thus the oldest fossil of the family..
FAMILY DIASPIDIDAE TARGIONI TOZZETTI

*Normarkcoccus*, new genus

**Type species:** *Normarkcoccus curtus* n. sp., by monotypy

**Occurrence:** India: western India Gujurat state, (Rust et al., 2010). Earliest Eocene (Ypresian).

**Etymology:** The genus is named after Benjamin B. Normark, for his contributions to understanding the systematics and phylogeny of the family Diaspididae. Gender: masculine.

**Diagnosis:** Body minute, head and thorax not separated, with two pairs of simple eyes on each side, dorsal eye on anterior margin of head, ventral eyes joining on venter; penial sheath short but needle-shaped apically.

**Species included:** *N. curtus* n. sp.

*Normarkcoccus curtus*, new species

(Figures 4.28; 4.29)

**Type locality:** Early Eocene, India, Gujurat, western India: Tadkeshwar lignite mines.

**Type:** Holotype Tad-135, alate male in a 4 x 5 x 0.5 mm dark orange, polished amber piece, specimen in relatively good condition but with thoracic structures damaged, wings spread backwards and touching together, body tilted in amber; accessible views: partial ventral and dorsal. India: Gujurat, western India: Cambay Shale Formation, Tadkeshwar lignite mines, coll. D. Grimaldi, P.C. Nascimbene, and H. Singh., deposited in the Birbal Sahni Institute for Palaeobotany, Lucknow, India.
Figure 4.28. Photomicrograph of *Normarkeoccus curtus* n. sp., dorsal surface of holotype AMNH Tad-135. See Materials and Methods section for abbreviations.
Figure 4.29. Details of *Normarkcoccus curtus* n. sp. A. Dorsal view of head, B. Ventral view of head, C. Leg, D. Ventral view of penial sheath.
**Etymology:** The species epithet comes from the Latin nomivative of “curtus” “shortened”, which refers to the shortened penial sheath compared to all the members of Recent Diaspididae.

**Diagnosis:** Same as genus.

**Description:** Body minute, spindle-shaped, total length 365 μm, widest at mesothorax (ca. 200 μm). Head: fused to thorax, ca. 80 μm wide. Ocular sclerites with two pairs of simple eyes each. Dorsal eyes on anterior margin of head, ventral eyes, meeting ventrally; with two lateral ocelli (10 μm). Head dorsally with a median crest, cuticle reticulate, bearing a few hair-like setae. Ventral ridges not observable.

Antenna 10-segmented, cuticle of pedicel reticulate, total length 225-250 μm; antennomere lengths (in μm) scape 16; pedicel 25, both scale and pedicel with short hair-like setae; flagellar segments III to X all filiform; III 25-30; IV 20-25; V 30; VI 25-30; VII 25-30; VIII 25-30; IX 25; X 15-20. Flagellomeres each with thick setae, probably fleshy but undifferentiated, ca. 15 μm long. Apical segment with two longer and thinner setae; one long, apical seta, apparently not capitate.

Thorax: prothorax membranous, cuticular ridges not visible. Thoracic structure not clearly visible, but dorsally, mesopostnotum long; ventrally, with a short basisternum.

Wings: forewings of neococcoid type, narrow base and apex rounded, ca. 420 μm long, 100 μm wide, symmetrical on mid-longitudinal axis; subcostal ridge extending from base of the wing to more than ¼ of wing length. Cubital ridge present, originating in basal quarter of wing, alar setae and sensoria absent, microtrichia present on wing membrane. Alar lobe present, receiving hooks of hamuli. Hamulohaltere narrow, ca. 40 μm long; with one hamulus.
Legs: robust, all of subequal length, cuticular reticulations absent. Foreleg: coxa ca. 30 µm long; trochanter and femur 70-80 µm long, 17 µm wide, with few short hair-like setae (ca. 15 µm long); tibia 155 µm long, proximally narrow (7 µm wide), distally twice the basal width, with a few hair-like setae, more numerous and spinose distally (tibial spurs); tarsus two-segmented, 35-40 µm long, 10 µm wide; tarsal digitules slightly clavate, shorter than claw; claw thin, 10 µm long, almost uncurved, claw digitules slightly clavate, reaching tip of claw, claw denticle absent.

Abdomen: relatively short and wide, ca. 172 µm long (but specimen tilted, 125 µm long without genital segment), 95 µm widest. Abdominal setae not visible except for pleural setae on last segments. Genital segment: Penial sheath subtriangular (87 µm long, 45 µm at base), covered with a layer of thin bubbles. Aedeagus pointed at apex, short, ca. 65 µm long. Eversible endophallus absent.

**Comments:** This new genus is referable to the Diaspididae based on the unseparated head and thorax; a fore wing that is almost symmetrical on the anteroposterior axis and having an extremely reduced venation; and thoracic structures that are almost unsclerotized; antennal shape, wherein the apical segment bears an apical seta; and the general shape of the legs, being enlarged between the tibia and tarsus. However, the extremely short penial sheath and the absence of capitate setae on the antennae (although two long setae are present) is different from all other members of Diaspididae. All Recent Diaspididae have a needle-type penial sheath, which the male inserts under the hard cover or test secreted by the female in order to reach the vulva. The females of this genus might have lacked an armored cover, or had a cover that was soft enough to be easily pierced.
In the morphological phylogenetic analysis, *Normarkcoccus* is not retrieved in the Diaspididae, but was found unresolved at the base of neococcoids. The family is well supported, for instance, by the presence of a long, spine-like penial sheath and by the presence of antennal capitate setae, features that are absent in *Normarkcoccus*. However, other features described above are conclusive in attributing this genus to the Diaspididae. Further character coding of these features, with a focus on the Diaspididae, should provided a better understanding of the relationships of this fossil genus.

**Phylogenetic results**

A total of 169 morphological characters were coded for all Recent taxa, including taxa for which only one of the sexual stages was available. In our study, all fossils had only macropterous males coded, as well as for one exception in Recent terminals (*Phenacoleachia* species b). Additionally, for some taxa macropterous males were either unknown, unavailable, or had with only apterous forms (*Marchalina*, *Phoenicococcus*, *Eumargarodes*, *Kuwania*, *Crypticerya*, *Puto superbus*, *Bambusaspis* and *Conchaspis agraei*). The morphological matrix is provided in Appendix B Table S4.2.

The MP analysis obtained from TNT, including 72 Recent taxa, 43 fossil terminals and seven outgroups, retrieved 11 most-parsimonious trees (MPT) of 1751 steps (Figure 4.30). Coccoidea is monophyletic and defined by the absence of mouthparts in the male, the membranous mesothorax, one pretarsal claw, and the absence of true ocelli in the macropterous male. Most of the Recent families with more than one terminal were retrieved as monophyletic except for the Monophlebidae and Pseudococcidae. As currently recognized, the family Eriococcidae is paraphyletic (but see Cook et al. [2002]).
Figure 4.30. Strict consensus of the 11 most parsimonious trees retrieved from TNT using 122 taxa (fossil + Recent) and 169 morphological characters, with non-ambiguous characters mapped. The tree has been divided into four parts (A, B, C and C). Percentage of morphological characters coded in indicated by the green pies. Unambiguous characters were mapped as dots on branches, with black dots = unique change, white dots= multiple changes. Fossil taxa are represented in bold. Bremer support and Jackniffe support >20 (P=36) are indicated at each node.
Matsucoccidae is the sister group to the remaining Coccoidea, followed by the Ortheziidae. The neococcoids were not retrieved as a monophyletic lineage in this analysis, probably because of a lack of morphological support (although molecular and genetic [sex-determining mechanism] support monophyly of Neococcoidea). As shown on node “b”, which refers to the neococcoids, the family Pityococcidae (traditionally considered an archeococcoid) is retrieved within the neococcoids, closely related to two Cretaceous genera *Turonicoccus* and *Pedicelloccocus*. The position of this clade is problematic as their males possess a row of multiple simple eyes, glandular pouches that differ from the male neococcoids. The divergence time analysis provided in Chapter V, with the same morphological matrix plus molecular data, retrieved this clade as the sister group to the fossil genus *Electrococcus*. These together are the sister group to a clade including all representatives of *Phenacoleachia* and Putoidae + neococcoids.

Fossils originally identified as Margarodidae, Matsucoccidae and Ortheziidae were placed within their respective families. Relationships of Xylococcidae and xylococcid-like fossil groups (Arnoldidae, Grohnidae, Serafinidae, Weitschatidae) are unresolved at the base of parts B-D of the cladogram. Additionally, the new Cretaceous genera *Priapococcus* and *Pseudoweitschatus* described in Chapter are also within this unresolved section (with *Pseudoweitschatus* a the sister genus to *Weitschatus*). The new Cretaceous family Kozarococcidae was retrieved as the sister group to two Cretaceous taxa, the new *Alacupacoccus* + Lebanococcidae. *Priapococcus* is retrieved as the sister taxon to Kozarococcidae but this relationship collapses when mapping character changes on the tree. The Late Cretaceous Jersicoccidae and the new, Early Cretaceous family Hodgsonicoccidae are sister families in this analysis, and collectively the sister group to
the Monophlebidae-Coelostomidiidae-Marchalinidae lineage. The male of Hodgsonicoccidae in Lebanese amber is a striking species with plesiomorphic features; it is very well preserved and the only large male coccoid known thus far from the Cretaceous.

The position of the clade including the taxa in parts C and D of Figure 4.30, shows the sister lineage to all the families, where males do not possess compound eyes. There is an extensive grade of 10 Cretaceous genera basal to the neococcoids and Putoidae + Phenacoleachiidae. These fossils show evidence of a larger diversity of lineages with males bearing a row of multiple simple eyes, now represented by only a few species in the Recent fauna.

The Pseudococcidae was not retrieved as monophyletic, specifically with *Antonina* being sister to *Ovaticoccus*, an Eriococcidae. Additionally, this analysis failed to recover Kermesidae as monophyletic. *Rosahendersona*, in the Coccidae, was found to be the sister group to *Ceroplastes*. The only new fossil in which relationships require further morphological coding is *Normarkcoccus*, a genus placed for now in the Diaspididae (see discussion under that genus), but retrieved in this analysis as unresolved in the neococcoids.

**Discussion**

The amber specimens that we studied were from the Early Cretaceous of Lebanon, mid-Cretaceous of Myanmar, and the Eocene of India and the Baltic region. From these, we have described a total of 16 new species in 14 genera (11 of them new) and 9 families (3 of them new). The amber from the Cretaceous Period provided most of the new specimens as well as most of the new diversity. Figure 4.31 is an updated summary
Figure 4.31. Diagram summarizing Coccoidea families known in the fossil record. Grey dots= previously described; white dots= known but undescribed ; stars= herein described.
of the coccoid fossil record at the family level, highlighting the many new records made in this study. Lebanese amber contains more families (9) than any other Cretaceous deposit, followed by Burmese (6) and New Jersey (5), although there is a significant number of New Jersey coccoids that need to be examined, and the commercial availability of Burmese amber will certainly provide yet more new taxa. Not surprisingly, Baltic amber (Eocene) preserves more fossilized coccoids – in 16 families – than any other fossil deposit, clearly due to centuries of study and exploitation of the world’s largest amber deposit, and years of research by Jan Koteja.

There is currently a total of 20 extinct families of Coccoidea (6 of them in Baltic amber, the rest from the Cretaceous). Of the 32 Recent coccoid families, 13 of them are represented in the fossil record, seven of which are known only from the Tertiary: Diaspididae, Eriococcidae, Kermesidae, Kuwaniidae, Margarodidae, Pityococcidae, and Putoidae. It might be expected that Margarodidae, as an archaeococcoid family, would occur in the Cretaceous, but the only known fossil is that of Heteromargarodes

*Hukamsinghi* n. sp. from the Eocene Cambay amber. Koteja (2008) considered that the Margarodidae were amongst the most successful archaecoccoid families, in stark contrast to their lack of fossils (even within Baltic amber). The exceptionally rare finding of a fossil margarodid is probably due to their hypogeous habits. In fact, *Heteromargarodes

*Hukamsinghi* n. sp. occurs in a piece of amber also containing some soil particles.

We also described from the same Cambay deposit a new genus of Diaspididae, *Normarkcoccus* n. gen., which has a short penial sheath, unlike its Recent counterparts. Fossils of Diaspididae are otherwise known from their waxy tests on fossilized leaves from the Early Miocene of New Zealand (Harris et al., 2007) and the Eocene in Germany.
(Wappler and Ben-Dov, 2008). Adult male Diaspididae occur in Baltic amber (Koteja Collection, Katowice) but still need to be described. As more Cambay amber with Coccoidea is found, it will be interesting to compare this diversity to that in the Baltic amber because there are some similarities between the two paleofaunas (Rust et al., 2010). Burmese amber (mid-Cretaceous) has the most diverse Cretaceous paleofauna (Ross et al., 2010) and is sufficiently abundant to be commercially marketed. A systematic search for additional Burmese amber coccoids will undoubtedly recover a significant number of new taxa. For this study, eight new species, six new genera and one new family were described from Burmese amber in the AMNH collection. Koteja (2004) described three genera and two families, as well as one genus incertae sedis (i.e., Marmyan), from the Burmese amber collection in the Natural History Museum, London. Additionally, Vea and Grimaldi (2012) described two new species in the genus Burmacoccus (Ortheziidae) based on nymphs, from Burmese amber. Thus, a total of 12 species and 11 genera in 6 families are now known from this Cretaceous deposit, with species assigned to Recent families represented by Coccidae (this study), Ortheziidae (Vea and Grimaldi, 2012), Pseudococcidae (this study) and Weitschatidae (this study).

Oddly, despite the presence of Matsucoccidae in the Early Cretaceous, in New Jersey amber (Koteja, 2000b), and their abundance and diversity in Baltic amber (Koteja, 1984; Koteja, 1986b), none have been found in Burmese amber. We predict that members of the Matsucoccidae will eventually be found in Burmese amber. Very significantly, the first definitive Cretaceous species assigned to the family Coccidae is reported here in Burmese amber, Rosahendersona prisca n. sp. Despite the unique combination of characters that defines it as a new genus, Rosahendersona bears several characters typical
of extant Coccidae (see comments in description, above). Other fossil Coccidae are known from Baltic amber (Koteja collection) but these still need detailed study. In addition, four genera in Burmese amber are *incertae sedis*: *Marmyan* Koteja (2004), *Alacupacoccus* n. gen., *Magnaelentis* n. gen. and *Pedicellococcus* n. gen. In general, most of the Coccoidea taxa in Burmese amber are morphologically diverse and quite different from the Recent fauna.

Lebanese amber has particular paleontological significance, since it is some 20-30 million years older (depending on the outcrops and deposits) than Burmese amber, and is highly fossiliferous. Koteja and Azar (2008) described eight coccoid species in seven genera and three new families from Lebanese amber. Our study adds four new species from this deposit, two of them in *Apticoccus* n. gen., placed with uncertainty in the Electrococcidae by Koteja and Azar (2008). Here, we erect a new family for the genus, *Apticoccidae* n. fam. However, the most significant discovery concerns two specimens here considered to be the earliest “mealybugs” (probably Phenacoccinae, Pseudococcidae), attributed to this subfamily based on the presence of only two pairs of simple eyes and the presence of wax filaments emerging from abdominal segments VII and VIII. Extant pseudococcids are ecologically highly successful, many of them engaging in intimate symbioses with ants (Schneider and LaPolla, 2011). They are members of the informal monophyletic group referred to as the neococcoids, (comprising some 90% of Recent species), and thus *Eopseudococcus* n. gen. in Lebanese amber, and *Geropseudococcus* n. gen. in Burmese amber, as well as the putative coccid *Rosahendersona* n. gen. in Burmese amber, provide evidence for a significantly more ancient origin and divergence time of the neococcoids than had been previously portrayed.
(e.g., Grimaldi and Engel, 2005). However, early presence is not evidence of radiation, as most taxa of organisms probably originated well before they radiated, and the question remains as to when the neococcoids underwent a period or periods of intense diversification. Fossil descriptions are often based on unique or rare inclusions, but the microscopic fidelity and diversity of morphological specializations in Cretaceous males clearly reveals that most of the taxa do not belong within any of the Recent families (Koteja, 2004; Koteja and Azar, 2008; herein). Our study confirms Koteja’s (2004) hypothesis that Cretaceous Coccoidea were significantly different from those of today based on the predominance of taxa with an elongate penial sheath, peculiar wing morphology, and minute size. Although most of these taxa have been described within archeococcoid groups, we found that the average body size of Cretaceous males was only 1020 μm long (median 935 μm, standard deviation 483 μm) and 277 μm wide (median 233 μm, standard deviation 138 μm). Recent archeococcoid families have been inter alia characterized by a significantly larger body size than that of neococcoids. There is only one significantly large archeococcoid species in the Cretaceous, Hodgsonicoccus patefactus n.sp., in Lebanese amber. Today, an elongate penial sheath appears to be a specialization associated with gall induction, or for taxa where the females have a hard test (e.g., Diaspididae, Coccidae), but is unknown in Recent archeococcoids. Many of the coccoids in Lebanese and Burmese ambers not only have an elongate penial sheath, some are definitively assigned to archeococcoid groups (e.g., Albicoccus, Burmacoccus, Kozarococcus, Priapococcus). There is no direct evidence or functional/adaptive explanation as to why an elongate penial sheath occurs in many Cretaceous taxa.
To conclude, although this study has provided substantial new knowledge on the fossil record of Coccoidea, the steady discovery of coccoids in these outcrops and in new sites will provide further understanding of coccoid evolution. Finally, perhaps the most crucial advance that can be made regarding the coccoid fossil record is with regard to the phylogenetic interpretation of the fossil taxa, which will require, at the very least, a rigorous analysis of male morphology.
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CHAPTER V

A TIME SCALE FOR SCALES:
DIVERGENCE TIME ESTIMATES INCORPORATING FOSSIL TAXA IN COCCOIDEA (HEMIPTERA: STERNORRHYNCHA)

Isabelle Vea and David Grimaldi

Abstract

Scale insects, or Coccoidea, comprise a superfamily within Hemiptera of some 8,000 described species. They are entirely phytophagous, mainly on angiosperms, and include some of the most damaging plant pests in agriculture and forestry. This has resulted in a rather specialized and sophisticated species-level taxonomy for the group, based mainly on the morphology of the adult female, but the higher-level phylogenetic relationships remain ambiguous, especially for the deeper node lineages (the grade of so-called archaeococcoid families). We assess whether fossil information, based on adult male morphology, can help resolve deep-node relationships in Coccoidea and then provide estimates of divergence times of the main lineages based on morphological and molecular analyses. Comparisons are then made to major biotic events in earth history. This study presents a total-evidence (vs. node calibration) approach to family-level phylogenetic assessment for the Coccoidea, including 169 morphological characters based on macropterous males (119 characters) and adult females (50 characters), as well as regions of the 18S, 28S and EF-1a genes. Taxon sampling includes 73 Recent and 43 fossil terminals covering 48 of the 54 recognized families (including those described in Chapter IV) in Coccoidea. Despite a very heterogeneous dataset and a large proportion of missing data, the analyses show that divergences among families within the Coccoidea – including the neococcoids (thought to have radiated as a result of the appearance of the
angiosperms)–preceded the angiosperm radiation by about 100 million years. The Coccoidea is estimated to have originated in the Late Triassic, ca. 220 Ma.

Introduction

The relationships of vascular plants and insects have a long history. Evidence of the association between plants and arthropods can be traced back to the Devonian when the first terrestrial ecosystems appeared (Kevan et al., 1975; Labandeira, 2002). Since the seminal and much cited work of Ehrlich and Raven (1964), who developed the theory that phytophagy had a profound effect on the radiation of insects and their host plants, new evidence continues to fuel the debate. Specifically, an understanding of how the interaction between plants and insects affects rates of speciation is one of the central questions in the field of coevolution. Mitter et al. (1988) hypothesized that the radiation of flowering plants provided ample opportunity for phytophagous insects to diversify, by increasing the rate of insect speciation. That study was based on comparisons between phytophagous sister groups, one feeding on angiosperms and the other on gymnosperms, the former being much more diverse. Today, herbivorous insects constitute one-fourth of all described species on Earth, and about one-third of all insects (Strong et al., 1984; Grimaldi and Engel, 2005). Another, complementary approach to understanding whether and how host-insect co-radiation occurred involves comparing the time scales for both insect and plant diversification (Janz, 2011). A few recent divergence time studies have, for example, demonstrated a time lag between the radiations of selected phytophagous groups of insects and their angiosperm hosts (McKenna et al., 2009; Percy et al., 2004).

Dating (i.e., divergence time) analyses have become common as more sophisticated analytical methods are developed and empirically used (Ronquist et al.)
2012a). They are becoming virtually routine, along with phylogenetic analyses, for addressing evolutionary questions such as biogeographic events, coevolution, diversification and extinction rates, responses to paleoclimatic change, key innovations etc. Until a few years ago, divergence time estimates could only be obtained using molecular data, with fossils simply being used to provide age calibration for exemplar lineages. This led to the “rocks vs. clocks” debate on conflicting results between paleontological and molecular studies (see review in Donoghue and Benton, 2007).

In addition to temporal information, fossils can also influence phylogenetic topology (Cobbett et al., 2007; Donoghue et al., 1989; Novacek, 1992). And, since most of the biodiversity that has ever existed is now extinct, fossils provide a necessary window into past diversity, and should be useful for phylogenetic inference. Because molecular data will never be available, almost all fossils studies are being developed to incorporate their morphological characters, the only way to directly assess both Recent and extinct taxa. For example, using fossil placement based on morphology a priori in analyses, to fix the age of calibration in termites, revealed a substantial difference in date estimates compared to using only molecular data with a posteriori node calibrations (Ware et al., 2010). After theorization (Gauthier et al., 1988; Donoghue et al., 1989; Huelsenbeck, 1991) and demonstrating the utility of incorporating fossil taxa in phylogenetic analyses (Wiens and Morrill, 2011; O'Leary and Gatesy, 2008), divergence time estimation is now utilizing fossil taxa as terminals, as an integral part of the analysis (BEAST: Magallón, 2010; Pyron, 2011; Wood et al., 2013; Ronquist et al., 2012a). This approach is important in groups where extinct and Recent relationships have never been assessed together.
Scale insects and mealybugs, or Coccoidea (referred throughout the text as scale insects), belong to the phytophagous suborder Sternorrhyncha, which also includes aphids (Aphidoidea), whiteflies (Aleyrodoidea) and plant lice (Psylloidea).

Sternorrhyncha are exclusively plant-sucking insects, with female scale insects having adopted an almost completely sedentary adult life on their host plant. Scale insects are among the most damaging plant pests in agriculture and horticulture and their species-level systematics (based almost entirely on adult female morphology) has been extensively studied and is very specialized. The superfamily includes over 8,000 described species (Ben-Dov et al., 2013) making this the most speciose group within Sternorrhyncha. Additionally, scale insects are perhaps the most specialized hemipteran phytophages, with an extreme sexual dimorphism in which the adult female is wingless and paedomorphic, mostly sedentary, and usually has fully functional mouthparts. The ephemeral macropterous adult males, developing via neometaboly (Bellés, 2011), do not feed after the second instar and live exclusively for reproduction. The Coccoidea have been traditionally and informally classified into two groups: (i) the monophyletic neococcoids, characterized for instance by the lack of abdominal spiracles and by a unique genetic mechanism of sex determination, paternal genome elimination (PGE) (Cook et al., 2002; Danzig, 1980; Nur, 1980; Yokogawa and Yahara, 2009). This group includes some of the most diversified families, such as the Coccidae, Diaspididae and Pseudococcidae, in addition to another 15 families (Gullan and Cook, 2007), and comprises many major pests. (ii) The archaeococcoids are represented by 15 Recent families, including the Ortheziidae, Monophlebidae, Margarodidae sensu stricto and sometimes the Putoidae, which together account for only 100 genera and 700 species.
They are characterized by the presence of plesiomorphic features, such as the presence of abdominal spiracles and, in the adult males, well-developed compound eyes and longer antennae (Schlee, 1969; Koteja, 1996).

Archaeococcoids are considered a paraphyletic grade (Miller, 1984; Foldi 1997; Cook et al., 2002; Hodgson and Foldi, 2005), and relationships among them were poorly resolved or understood (Gullan and Cook, 2007) until recently (Hodgson and Hardy, 2013).

Because of the extreme sexual dimorphism and the significant role of the conspicuous feeding adult females in human activities, they are the stage used for taxonomic work. In contrast, the short-lived (2-5 days) adult males are, for a large majority of genera and species, unknown. Although not an issue for species identification and delineation (but see Gwiazdowski et al. [2011]), this situation became problematic for phylogenetic studies, since the paedomorphic females have many highly reduced features (including the loss of appendages in some families), and can also dramatically differ from family to family. This situation challenges the homologizing of morphological characters. Adult male morphological characters were however found to be phylogenetically more informative than that of females, especially at the family level (Hodgson and Foldi, 2005; Hodgson and Hardy, 2013), but taxon sampling of males is sparse for many genera and even some families. Gullan and Cook (2007) actually foresee a better understanding of scale insect phylogeny through molecular data only, but this approach becomes an issue for interpreting the large diversity of scale insect fossils, preserved largely as males. Fortunately, the last decade has been quite fruitful in our knowledge of male morphology, especially in the archaeococcoid families (e.g., Hodgson and Foldi, 2006; Hodgson et al., 2007; Hodgson, pers. comm. and Chapter III).
Fossil scale insects are diverse and abundant, preserved mostly in amber, in deposits around the world from the Early Cretaceous to the Miocene, ca. 130-20 Ma. In some amber deposits, such as the Turonian-aged amber from New Jersey (90 Myo), they are one of the most abundant and diverse groups of insects (Grimaldi et al., 2000). Fossil coccoids have been extensively studied, mostly by Koteja (Koteja, 2000a; Koteja, 2004; Koteja, 2008; Koteja and Azar, 2008; and Chapter IV). However, in contrast to the taxonomy of Recent scale insects, fossils are, with a few exceptions, entirely based on adult males. To date, fossil species that have been described represent 19 extinct (including three new families described in Chapter IV) and 33 Recent families. The study of fossil taxa in ambers has revealed a surprising diversity, especially from the Cretaceous (e.g., Koteja, 2000a; Koteja, 2004; Koteja and Azar, 2008; Chapter IV). Koteja proposed a scheme of relationships amongst Recent and extinct families (Koteja, 2000b; summarized in Grimaldi and Engel, 2005), but no quantitative phylogenetic analysis has been undertaken until very recently (Hodgson and Hardy, 2013).

Despite the challenges of taxon sampling for male scale insects, and of studying minute amber inclusions, Coccoidea is an excellent group for exploring the diversification of a major group of phytophagous insects. There have been two main hypotheses proposed with regard to scale insect origin and evolution. Borchsenius (1958) hypothesized that most of the families were established before the Cretaceous and that the original host plants were gymnosperms. The alternative hypothesis favors a recent diversification of scale insects, being a consequence of the flowering-plant radiation and giving rise to the major neococcoid families, the most diverse today (Hoy, 1962; Danzig, 1980). In the 30-50 years since these hypotheses were proposed, huge advances have
been made, not only in DNA sequencing and in the discovery and description of adult males and fossils, but also in analytical methods. Therefore, the time seems appropriate to assess any impact of angiosperm radiation in the Cretaceous on the diversification of Coccoidea. This study used morphological characters of 73 Recent and 43 fossil exemplar taxa, and sequences from three nuclear markers, to estimate divergence times of major lineages (families and family-groups) of Coccoidea.

**Materials and methods**

**Taxon sampling**

Taxon sampling was defined according to the particular situation found in the systematics of scale insects. First, fossil species are only represented by macropterous males. Second, adult males are generally poorly known for Recent taxa. As a result, species (or genera) were prioritized in families for which adult males were known and that could either be collected for DNA sequencing or, where sequences were already available on Genbank. Additionally, in order to obtain a better morphological representation of the superfamily, also included were Recent representatives without molecular data available but with complete morphological character coding. This was done to potentially optimize fossil placement, by increasing morphological representation across the superfamily. Finally, as many archaeococcoid families as possible were represented, since so many of the Cretaceous fossils were clearly archaeococcoids. The final taxonomic sampling included 115 ingroup terminals and seven outgroups (Aphididae and Adelgidae). Within the ingroup, a total of 48 families are represented for at least one taxon. For the extinct taxa, a total of 43 terminals were sampled, among which 25 are species described by Koteja and 16 newly described species (Chapter IV).
Tables 5.1 and Table 5.2 provide lists of sampled Recent and fossil terminal taxa, respectively.

*Morphological characters and molecular data*

We used the morphological matrix coded and presented in Chapter IV of this dissertation (see Material and Methods of Chapter IV and Appendix B Table 4.2). This matrix consists of 169 characters defined for macropterous males (119 characters) and adult females (50 characters). All fossils had only macropterous male characters coded.

Specimens used for molecular sequencing were either preserved in 100%, 70% ethanol, or acetone. Total genomic DNA was extracted using a DNeasy tissue extraction kit (Qiagen), following the manufacturer’s instructions, except for the following: whole specimens were left in lysis buffer and proteinase K overnight, two elutions of 50 microliters were obtained at the end of the extraction, and the cuticle of each specimen was retrieved from the extraction column for slide preparations and identification.

Three nuclear markers were amplified and sequenced for this study: 18S, two regions of 28S (D2-3 and D10) and a region of EF-1 alpha. Appendix C Table S5.1 provides the primers used for amplification of the four markers; Genbank accession numbers (and temporary numbers for unaccessioned sequences) are available on Table 5.2. PCR amplifications were used a Mastercycler ep Gradient S (Eppendorf) and consisted of 25 µm reactions with Illustra Ready-To-Go PCR beads (GE Healthcare), 1 µm of each primer (x10 dilution) and 2 to 4 µm of DNA template, depending on the quantity of DNA retrieved from the extraction. For 18S and 28S fragments, PCR conditions published in Hardy et al. (2008) were used. The EF-1a fragment was amplified
Table 5.1. List of Recent taxa used in this study, classified into currently recognized families.

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<th>Family</th>
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<th>28S D2</th>
<th>28S D10</th>
<th>EF-1a</th>
<th>Species for morphological coding</th>
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<td>Aclerda sp.</td>
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<td>---</td>
<td>---</td>
<td>A.arundinariae</td>
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<td>Adelgest</td>
<td>A.tsaugae</td>
<td>xxxX101</td>
<td>---</td>
<td>---</td>
<td>A.tsaugae(m3)</td>
<td>A.arundinariae</td>
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<tr>
<td>Adelgidae</td>
<td>Adelgesa</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>A.abisites</td>
<td>P.flocus</td>
</tr>
<tr>
<td>Adelgidae</td>
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<td>Lebanese</td>
<td>125</td>
<td>Vea and Grimaldi, in prep.</td>
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<td>125</td>
<td>Koteja &amp; Azar 2008</td>
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<td><em>Marmyan barbara</em> Koteja</td>
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<td>Age (Mya)</td>
<td>Reference</td>
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<td>Koteja &amp; Poinar 2001</td>
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<td>Vea and Grimaldi, in prep.</td>
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<td>Vea and Grimaldi, in prep.</td>
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<td>Baltic</td>
<td>45</td>
<td>Koteja 2008</td>
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using two sets of primers covering two overlapping regions, which resulted in a fragment of ~ 1080 pb. Conditions for PCR follow that of Morse and Normark (2005) and Downie and Gullan (2005) PCR products were purified using AMPure magnetic beads (Agencourt) and cycle-sequenced with the BigDye 1.1 Terminator Reaction Mix (Applied Biosystems, Inc), the same set of primers as PCR. This protocol allowed a faster cycle sequencing program and the use of less BigDye. Cycle sequenced products were purified using CleanSeq (Agencourt) or ethanol precipitation. Sequencing was performed using an ABI 3730xl DNA Analyzer. Sequences were then compiled and edited using Geneious 5.1.7 and saved in separate fasta files for further analyses. Sequence alignments were performed using MAFFT (Katoh et al., 2002) through the Geneious platform. Introns from EF-1a were removed and the gene was partitioned by codon position (3 partitions). All three markers and the morphological dataset were concatenated for further analyses.

Phylogenetic analyses

Two datasets were analyzed for this study: (i) molecular and morphological data for Recent taxa only (80 taxa and 4019 characters), and (ii) morphology and molecular data for fossil and Recent taxa (123 taxa and 4019 characters). For each dataset, analyses used Maximum Parsimony (MP) implemented in TNT (Goloboff et al., 2008), Maximum Likelihood (ML) with RAxML 7.2.7 (Stamatakis, 2006), and Bayesian Inference with MrBayes 3.2.1 (Ronquist et al., 2012b), through the Cipres Science Gateway portal (Miller et al., 2009) for the latter two programs. For the model-based analyses, substitution models were first assessed with jModelTest 2.1.1 (Darriba et al., 2012) using 11 substitution schemes with an ML base tree; the first selected models under AIC and
BIC were TIM3ef+I+G for 18S, TVM+I+G for 28S. EF-1a was partitioned by 3rd codon position and selected models were TPM2+I+G and TIM3+I for partition codon position 3. All selected models are not implemented in MrBayes 3.2.1 and RAxML 7.2.7, so GTR+I+G for Bayesian Inference and GTR+G for Maximum likelihood analyses were also used for the three partitions. Clade supports were estimated with Jackknife support (33% resampling) for TNT, Bootstrap values for RAxML 7.2.7, and posterior probability for MrBayes 3.2.1.

**Divergence time estimates**

Divergence times for major lineages and phylogenetic hypotheses were co-estimated using a Bayesian-relaxed clock method with MrBayes 3.2.1. Two analyses were carried out: (a) first, a divergence time estimation was inferred using only Recent taxa in which seven node calibrations were applied to the following families: Coccidae, Diaspididae, Margarodidae, Matsucoccidae, Ortheziidae, Putoidae and Xylococcidae, in addition to Coccoidea and the root. For each node representing the families above, an age prior was assigned based on known fossils that could be definitively assigned to these Recent families (see Appendix C Table S5.2). (b) A total evidence approach was followed, where the 43 fossil terminals were incorporated into the analysis. Only the root and Coccoidea had node calibration priors applied as in approach (a), but all other age priors were set for fossil terminals as fixed ages (see Table 5.2 for ages). Both analyses used a relaxed IGR model detailed in Ronquist et al. (2012a). Preliminary non-clock and strict-clock analyses were performed with Coccoidea as a topological constraint, in order to define prior values for the IGR variance and the clock rate.
Four replicates of 10 to 20 million generations were run for each MrBayes analysis at an initial temperature of 0.2 for preliminary analyses and 0.1 for the calibrated ones. Each analysis convergence was considered achieved when the average standard deviation of split frequency was below 0.05.

Results

Taxon and data coverage

The final dataset had a 23.25% total coverage, with very heterogeneous datatyp across our sampling. Of the 123 terminals, 44 (35.8%) had only male morphology coded, which correspond to the 43 fossil taxa and a species of Phenacoleachia; 40 (32.5%) had all types of data available; 30 (24.4%) had only morphological characters from both adult males and females; 7 (5.7%) had both molecular data and female morphology; and only one each (0.8%) had either just female morphology or molecular data coded. Among terminals with molecular data available, data coverage was uneven among markers (see Appendix C Table S5.3). Because morphological characters of males were partially coded (not all features were visible), fossil taxa had an average of 1.88% of the complete matrix (molecular and morphological data), and 44.7% of the complete morphological matrix. While 2% may seem a low value, this is not a purely statistical issue, but it rather depends on the information content of the preserved characters. Also, preservation of nearly 50% of the full array of morphological characters is quite good in paleontology when Recent taxa are involved.
Phylogenetic results

Dataset (i): Morphology + molecular data for Recent taxa

When only considering Recent taxa and using a combined approach, the parsimony analysis retrieved 66 MPT of 10,870 steps, CI=42 and RI=56 (Figure 5.1). In this result, Coccoidea is monophyletic. The monophyly of most families is also retrieved except for the Monophlebidae and Diaspididae. For the latter two, the nodes are unresolved with the Coelostomidiidae and Phoenicococcus, respectively. Additionally, all the members of Margarodidae were retrieved as monophyletic except for Eumargarodes, which was included in the unresolved Coccoidea node (clade a). This genus is the only sampled Margarodidae with available DNA sequences, but unknown male morphology. Within the Coccoidea, the largest resolved clade (clade b) includes the Steingeliidae (but only represented by one Recent terminal), being sister group to clade c, which includes Phenacoleachiidae + Putoidae, sister to Pityococcidae + neococcoids (clade d). The neococcoids (clade d) form a monophyletic lineage and, when comparing to the parsimony analysis using only morphological characters (see Figure 4.30 in Chapter IV), the main relationship conflict is the placement of Pseudococcidae. The topology retrieved from the ML analysis of Recent taxa, presented in Figure 5.2, retrieved Coccoidea as monophyletic (clade a). All families with more than one terminal were monophyletic, except for Diaspididae and Coccidae, retrieved as paraphyletic by the inclusion of Phoenicococcus + Conchaspidiae, and Aclerda respectively. In Figure 5.2, two main lineages are retrieved within the Coccoidea: clade b including all members of scale insects with adult males bearing well-developed compound eyes; and clade c including the rest of scale insects, namely the families for which adult males bear simple
Figure 5.1. Strict consensus of the 66 MPT obtained from TNT, including 80 Recent terminals, 169 morphological characters, 18S, 28S and EF-1s partial regions. Length=10870, CI= 42, RI=56. Characters 10, 64 and 105 are ordered. Bootstrap support > 20% is indicated below branch as follow: one small star= 20-39%; two small stars= 40-59%; three small starts= 60-79%; four small stars= 80-89%; one large star= 90-100%. Letters at nodes represent clades discussed in the text.
Figure 5.2. Topology obtained from Maximum Likelihood analysis using RAxML, including 80 Recent terminals, 169 morphological characters, 18S, 28S and EF-1a partial regions. Rapid bootstrap, 5000 replicates. Bootstrap support values on nodes. Letters at nodes represent clades discussed in the text.
eyes (multiple or only two pairs). In clade b, Matsucoccidae is sister family to Ortheziidae, together being sister to a clade comprising Margarodidae, sister to Kuwaniidae + Marchalinidae + Xylococcidae + Stigmacoccidae + Callipappidae + Coelostomidiidae + Monophlebidae. The latter two are sister clades. Clade c has, as in the parsimony analysis (Figure 5.1), Steingelia sister to the rest of the members of clade c. The lineage including Phenacoleachia and the Putoidae is sister to the neococcoids (clade d). The latter, however, were found to include Pityococcus, as in the parsimony analysis based on morphological characters (Figure 4.30). Here, the genus is found as sister group to Stictococcus, and therefore imbedded in the BSE (“Beeoniidae-Stictococcidae-Eriococcidae”) clade defined in Cook and Gullan (2004).

Figure 5.3 is the majority-rule consensus summary of the non-clock Bayesian analysis, including Recent terminals only. Once again, Coccoidea is monophyletic as are all families with the exception of Diaspididae. The neococcoids in the traditional sense are monophyletic but there is no resolution as to its sister group, although the all-compatibility summary (Appendix C Figure S5.1) indicates that Pityococcus is the sister lineage to the neococcoid (as retrieved in the ML topology), a result that accords more with the traditional views. Additionally, no resolution was found in the majority consensus for the four deepest nodes of Coccoidea. When examining the all-compatibility summary, Matsucoccidae is sister to the rest of Coccoidea and Ortheziidae is not related to Matsucoccidae but retrieved as sister to clade c of Figure 5.2, making the Ortheziidae more closely related to the neococcoids than the archaeococcoids. In Hodgson and Hardy (2013), a phylogenetic analysis at the family level, based on macropterous male
Figure 5.3. Majority-rule consensus summary of the non-clock analysis performed with MrBayes 3.2, including 80 Recent terminals, using 169 morphological characters (MK model), 18S, 28S and EF-1a partial region. EF-1a was partitioned with 3rd codon position (partitioned analysis, unlinked GTR+G+I). Topology constraint applied to Coccoidea. Column next to taxon name represents proportions in percentage of data completeness for the following type of data: Total completeness, morphological characters, male morphology only, female morphology only, molecular data, 18S only, 28S only, EF-1a only. Values for each column are provided in Appendix C Table S5.3. Posterior Probability values > 20% are indicated below branch as follow: one small star = 20-39%; two small stars = 40-59%; three small stars= 60-79%; four small stars = 80-89%; one large star= 90-100%.
characters only, retrieves Ortheziidae as sister group to the Matsucoccidae, corroborating the ML topology (Figure 5.2).

In order to provide an overview of data “completeness” for each recent terminal taxon, Figure 5.5 has small bar charts representing eight columns for each terminus. Each of them shows the proportion for the following types of data (from left to right): Combined data, all morphology, male morphology, female morphology, all molecular, 18S, 28S and EF-1a. There is no distinct pattern or correlation in the placement of terminals with the proportions of partitioned data. However, irresolution in the majority-rule consensus summary (excluding node with PP < 50%) seems to be correlated with the absence of molecular data.

**Dataset (ii): Morphology + molecular data for Recent and fossil taxa**

The parsimony analysis resulted in 8 MPT of 11,212 steps (CI=40, RI=57), for which the strict consensus is presented in Figure 5.4. When adding fossil terminals in the parsimony analysis, Monophlebidae, Kuwaniidae, Diaspididae are found not monophyletic. Additionally, Clade b as defined in Figure 5.2, which includes all scale insects with compound eyes is not now monophyletic because of the inclusion of the Ortheziidae in clade c (defined in Figure 5.2). The family Ortheziidae + fossils including Kozarococcidae, Lebanococcidae and *Alacupacoccus* are found related to the Steingeliidae, family with males bearing a row of multiple simple eyes. The placement of the Ortheziidae in this resulting topology is quite peculiar and conflicts with the morphological only parsimony analysis (Figure 4.30 in Chapter IV). Additionally, the genus *Stictococcus* is retrieved as sister group to the fossil family Apticoccidae and therefore making the neococcoids paraphyletic.
Figure 5.4. Strict consensus of the 8 MPT obtained from TNT, including 123 terminals (fossils and recent), using morphological characters and molecular data. Length= 11212, CI=40, RI=57. Characters 10, 64 and 105 were ordered. Jackknife support > 20% is indicated below branch as follow: one small star= 20-39%; two small stars= 40-59%; three small starts= 60-79%; four small stars= 80-89%; one large star=90-100%. Fossil taxa are in bold.
The combined ML topology is presented in Figure 5.5. All families are retrieved as monophyletic except for Diaspididae (including *Phoenicococcus*) and Coccidae (including *Aclerda*). In this result, the division into two clades as in the ML topology without fossils, is not retrieved because of the position of Ortheziidae (along with the fossil Burmacoccidae, Kozarococcidae, Lebanococcidae and *Alacupacoccus*) and is now sister group to clade c as defined in Figure 5.2. The addition of fossils also results in *Pityococcus* now excluded from the neococcoids (compared to the extant taxa ML analysis) and being related to the fossils *Electrococcus*, *Grimaldiella*, *Pedicellococcus* and *Turonicoccus*, together sister lineage to the rest of the members with macropterous males bearing simple eyes.

Divergence time estimates

In addition to the non-clock analysis (Figure 5.3), a strict-clock analysis (Appendix C Figure S5.2) was obtained and both were used to define priors for the IGR model. Branch length variance between both majority-rule topologies was calculated using the R script provided in Ronquist et al. (2012a). Plot of the R analysis is presented in Appendix C Figure S5.3. The graph slope was used as a median value to set up the IGR variance prior. The strict-clock tree height was used to define the clock rate prior (see Ronquist et al., 2012a for more details).

Node-calibrated analysis

The node-calibrated analysis result including only Recent taxa is presented in Figure 5.6 as the all-compatibility summary tree from MrBayes 3.2.1. Monophyly is retrieved for all families except Monophlebidae, where *Palaeococcus* appears as the sister group to Marchalinidae. Relationships are the same as for the non-clock analysis
Figure 5.5. Topology based ML analysis with RAxML, including 123 terminals (fossils and recent), using morphological characters and molecular data. Fossil taxa are in bold. An MK model was used for morphological characters, GTR+G as separately partitioned for molecular data. EF-1a was partitioned with 3rd codon position. Bootstrap support values > 20% are indicated at the node.
Figure 5.6. Estimates of divergence times in Recent Coccoidea inferred with MrBayes 3.2, including 80 terminals, using both morphological and molecular data. Node calibrations based on fossils belonging to Recent families indicated by an arrow. Posterior probability > 20% is indicated below branch as follow: one small star= 20-39%; two small stars= 40-59%; three small starts= 60-79%; four small stars= 80-89%; one large star= 90-100%. Letters at nodes represent clades discussed in the text.
(Figure 5.3) except that Monophlebidae is monophyletic in the former topology. Diaspididae is retrieved as monophyletic in the calibrated analysis because of the topology constraint applied for this family to set a node calibration prior. This analysis supports the division of Coccoidea into the two main lineages also found in the ML analysis only using Recent taxa. Within clade b, which includes the archaeococcoids, where males bear compound eyes, Ortheziidae is sister family to Matsucoccidae. In clade c, Pityococcus + Steingelia are retrieved as sister group to the rest of clade c, followed by the lineage comprising Phenacoleachia + Putoidae, which are in turn sister group to all neococcoid families.

This analysis also estimates the split between Coccoidea and Aphidoidea at 293.5 Ma [95% interval: 292, 300] (earliest Permian), with the basal-most divergence within Coccoidea (clade a) occurring approximately 230 Ma [95% interval: 180.6, 283] (Middle Triassic). Direct evidence for such a Triassic divergence comes from the stem-group Triassic aphid Creaphis, although an early Permian coccoid-aphid divergence far exceeds any direct, fossil evidence. Most of the Recent families were either established or had diverged from their sister group by 100 million years. More particularly, the neococcoid lineage originates 197 Ma [95% interval: 144, 254]. By 100 Ma, the Pseudocccidae have probably already diversified. The splits of the Aclerdidae with Coccidae, Dactylopiidae and Eriococcidae from the Palaearctic, BSE clade and lineage that will give rise to the Conchaspididae, Phoenicococcidae and Diaspididae, have already taken place. Most of the families in the archaeococcoids are also already in place in the mid-Cretaceous.
Total evidence divergence time analysis

When incorporating fossil taxa into the divergence time analysis, only applying a topology constraint for the ingroup and a node calibration prior at the root of the tree, most of the main relationships of Recent families remained the same as in the node-calibrated analysis (Figure 5.7). Diaspididae is however not retrieved as monophyletic when a topology constraint is not specified. The topologies of the morphological analysis (Figure 4.30) and total evidence Bayesian trees differ in the deep-node relationships, especially among the families at the base of the trees. For instance, the Matsucoccidae were found sister group to the rest of the Coccoidea in Figure 4.30, whereas the total evidence result favors a relatedness between Matsucoccidae and Ortheziidae. Additionally, the two main lineages (clade a and b) diverging within Coccoidea are again retrieved, as opposed to the general pectinate topology in Figure 4.30. In the dated phylogeny, Matsucoccidae being sister family to Ortheziidae agrees with the hypothesis found in Hodgson and Hardy (2013) using only macropterous males. The other lineage within clade a is composed of the Margarodidae, Callipappidae, Stigmacoccidae, Kuwaniidae, Monophlebidae, Coelostomidiidae, Marchalinidae and all Xylococcidae and their fossil relatives. The Margarodidae + the Cretaceous family Grimaldiellidae (Late Cretaceous) are the sister to the rest of the clade. This position of Grimaldiellidae, however, significantly differs from the standpoint of morphology only, where this family is more closely related to fossil taxa with ocular sclerites having multiple simple eyes. As inferred in Hodgson and Hardy (2013), the Monophlebidae and related families form a clade with the Xylococcidae (plus extinct relatives), as well as Callipappidae,
Figure 5.7. All-compatibility tree of estimated divergence times obtained from MrBayes using the total-evidence approach, including 123 terminals and using both morphological characters and molecular sequences; all fossils (in bold) are treated as terminal taxa and calibration was defined. Arrows on 26 indicate an increase (upward) or decrease (downward) of 95% credibility interval and is the median age is younger (right) or older (left), compared to the calibrated analysis (Figure 5.6). Posterior probability > 20% is indicated below branch as follow: one small star= 20-39%; two small stars= 40-59%; three small starts= 60-79%; four small stars= 80-89%; one large star= 90-100%. Letters represent clades discussed in the text.
Stigmacoccidae and Kuwaniidae. The second lineage within Coccoidea is clade \textit{b}, which includes the neococcoids (Danzig, 1980; Nur, 1980, Cook et al., 2002; Gullan and Cook, 2007; Yokogawa and Yahara, 2009). Most of the relationships retrieved within this group corroborate the results of Yokogawa and Yahara (2009), with the Pseudococcidae being sister group to the rest of the neococcoids (Miller, 1984; Cook and Gullan, 2002), and the remaining neococcoids divided into two main clades: one comprised of the Coccidae, Kermesidae, Asterolecaniidae, but also Kerriidae, Lecanodiaspididae, Cerococcidae, and Aclerdidae; and the other lineage comprised of the Diaspididae, Conchaspisidae, Phoenicococcidae, which together form the sister group to the BSE clade (“Beesoniidae-Stictococcidae-Eriococcidae”, Cook and Gullan, 2004) and Gondwanan eriococcids. Dactylopiidae and the Palaearctic eriococcids are sister groups. Although each lineage within Clade \textit{b1} is similar to those in Cook and Gullan (2004), their relationships differ. In the present study, the neococcoids are sister group to Recent Putoidae + Phenacoleachiiidae. All members of Putoidae were previously included in the Pseudococcidae, but male morphology (Hodgson and Foldi, 2005), plesiomorphic cytology (Hughes-Schrader, 1944) and molecular analyses (Gullan and Cook 2007; Cook et al., 2002) all indicate that it should be a separate family, and the split was recently reemphasized in Williams et al. (2011). The relationship of Putoidae to Phenacoleachiiidae is supported by male morphology (Hodgson, 2002). Steingeliidae is the sister group to Putoidae + Phenacoleachiiidae + neococcoids and Pityococcidae is a sister group to all of these (all other members of clade \textit{b}), which differs from the analysis of Hodgson and Hardy (2013).
In Figure 5.7, several fossil stem groups are retrieved at the base of various lineages: group I includes Burmacoccidae, Lebanococcidae, Kozarococcidae and *Alacupacoccus*. These families and genera are from Burmese and Lebanese ambers. Group I, along with the Matsucoccidae and Ortheziidae forms Clade a1, which is estimated to have originated in the Late Triassic ca. 213 Ma [95% interval: 180, 239]. Group II comprises the Pityococcidae, *Turonicoccus* and *Electroccoccus* both placed in the Electrococcidae (Koteja, 2000a), as well as *Pedicellococcus*. The fossil *Pityococcus* is from mid-Eocene Baltic amber, the other genera occur in Early Cretaceous deposits. Group II originated in the Early Jurassic ca. 192 Ma [95% interval: 153, 227] and seems to have diversified early in scale insect evolution, with only *Pityococcus* surviving from this group. Group III comprises families preserved in Early Cretaceous Lebanese amber (Albicoccidae and Apticoccidae), and the Recent, apparently relict, Steingeliidae. Steingeliids occurred into the Early Cretaceous, and the origin of the family is estimated at Late Jurassic in age 153 Ma [95% interval: 135, 180]. Today, the family includes genera occurring in the Nearctic (*Stomacoccus*), Palaeartic (*Steingelia*) and Australia (*Coniferococcus*, *Araucaricoococcus*), although their relationships have never been assessed. Group IV is subordinate within the neococcoids, and sister group to the clade comprised of the Diaspididae + Conchaspididae + Phoenicococcidae + Eriococcidae + Diaspididae. *Kuenowicoccus* was described as an eriococcid from Baltic amber (Koteja, 1988); *Inka* is from Late Cretaceous Siberian amber (Koteja, 1989b) and *Pennygullania* from Early Cretaceous Lebanese amber (Koteja and Azar, 2008).

Isolated fossil groups include the following: Grimaldiellidae (Late Cretaceous of New Jersey) is sister to the Margarodidae; Labiococcidae (as *Solicoccus*) (New Jersey)
seems to be related to the clade Phenacoleachiidae and Putoidae. The new fossil genus *Magnaelentis*, related to *Phenacoleachia* was described as *incertae sedis* from mid-Cretaceous Burmese amber (see Chapter IV). *Kukaspis*, a genus from mid-Cretaceous Alaska amber, was retrieved as the sister group to the Putoidae. Although *Rosahendersona* was described as a definitive Coccidae (Chapter IV), a placement for which parsimony and ML analyses agree, the Bayesian-dated phylogeny positions it at the base of a clade formed by Aclerdidae and Coccidae.

Finally, it is unclear how the Xylococcidae and xylococcid-like families relate to each other. The sister lineage to the Monophlebidae and related families comprise the Xylococcidae, Kuwaniidae, Callipappidae and Stigmacoccidae. All fossils from Baltic amber described by Koteja (2008) and discussed as related but separated from Xylococcidae are also included in this lineage: Serafinidae, Weitschatidae, Arnoldidae and the new *Pseudweitschatus* (described in Weitschatidae, Chapter IV) are directly related to the *Xylococcus*. However, Grohnidae and the new *Priapococcus* (described in the Xylococcidae, Chapter IV) are respectively closer to Callipappidae + Stigmacoccidae and Kuwaniidae. Except for *Grohnus*, all xylococcid families from Koteja (2008) could potentially be synonymized with Xylococcidae, although it would imply the redefinition of the family, incorporating a larger morphological diversity in this family.

**Discussion**

*Missing data*

Three main situations are encountered in our data matrix: (i) 32.5% of the taxa have both morphological characters and molecular sequences, with a variation in marker coverage; (ii) 24.4% of taxa have only morphological characters, with few missing cells
but no molecular data, which gives an average of 4% of total completeness for these taxa; (iii) all fossil terminals are coded only for male morphology with an average of 2% of total completeness (45% when only considering morphological characters). In previous empirical and modeling studies, the presence of non-randomly distributed missing data in the matrix can lead to problems in tree reconstruction and divergence times estimates (Lemmon et al., 2009). However, this can be countered if any informative signal is present in the matrix (Lemmon et al., 2009; Wiens, 2006; Wiens et al., 2009). Ronquist et al. (2012a) argued that, because adding fossils did not affect the relationships of their extant taxa, then missing data had little effect on the results. Also, the placement of highly incomplete taxa is shown to be more accurate when the overall number of characters is high for parsimony, Maximum Likelihood (Wiens, 2003) and Bayesian methods (Wiens and Moen, 2008). More characters simply increase the probability that some of them will provide informative signal.

Although there is no other means other than morphology with which to assess whether fossils are accurately placed, consistency in fossil placement among analytical methods also provides some assessment. In this study, the following fossil relationships were consistently retrieved in both parsimony and Bayesian approaches: *Eomatsucoccus* in Matsucoccidae; *Cretorthezia, Palaeonewsteadia, Protorthezia* in Ortheziidae; the fossil *Xylococcus grabenhorsti* in the Xylococcidae; the fossil *Pityococcus moniliformis* was always with Recent *Pityococcus*; and *Palaeoesteingelia* and *Steingelia cretacea* in the Steingeliidae. Additionally, the new fossil genera described in Pseudococcidae resulted as sister groups to the rest of Pseudococcidae in the total-evidence analysis. The fossil family Kozarococcidae was among the fossil taxa whose relationships varied among
methods, related to the Xylococcidae-groups in the TNT analysis based on morphology but closer to the Ortheziidae with ML and Bayesian inference (in the end, for the total-evidence analysis including all data, it resulted as the sister lineage of Matsucoccidae + Ortheziidae). Our study also involved Recent taxa with only morphological characters, all of which were accurately placed despite their 4% completeness. Finally, monophyly of most families was retrieved across analyses, with a few exceptions such as the Diaspididae, which always included the Phoenicococcidae, where monophyletic lineage could not be obtained except in the calibrated analysis where the family was topologically constrained. This seems to be caused by the absence of male morphology in the Phoenicococcidae, but this family was hypothesized to be related to the Diaspididae (Gullan and Cook, 2007), although additional study is needed. Finally, the most versatile taxon among analyses was Pityococcus, retrieved within the neococcoids in the parsimony morphological analysis (fossil+Recent) and when only Recent taxa were analyzed, but found as related to either Steingelia or other fossil genera when fossils were included in the combined-data analyses. Although, no DNA sequences were available for Pityococcus, the addition of fossils could help place this genus in a more generally accepted position within the phylogeny (Hodgson and Hardy, 2013).

Cobbett et al. (2007) investigated the effect of including fossil taxa for parsimony analyses, on relationships, number of most-parsimonious trees, branch support (jackknife and bootstrap) and CI and RI. That study used 45 published morphological datasets, and concluded that the largest effect was the reduction of total branch support. In our study, missing data was a result not only from extensive fossil terminals, but also because of the peculiar biology and taxonomy of scale insects. When comparing datasets (i) and (ii) for
parsimony methods, the incorporation of fossil terminals significantly reduced the resolution of deeper nodes. In statistical methods, most of the ML analyses retrieved very low bootstrap values. One significant thing to note is that RAxML does not allow an ordering of multi-state characters. Also, the models used for the molecular sequences (GTR+G) might not have been appropriate. Results from the Bayesian total-evidence result have deep nodes with low posterior values. However, terminal nodes or branches of fossils and Recent taxa with only morphological characters had relatively high support values. The same pattern was found for the calibrated analysis. The increasing number of studies with large taxon and gene sampling or studies including fossil taxa inevitably begins with incomplete data.

_Divergence time estimates_

The node-calibrated and total-evidence analyses (Figure 5.6 and 5.7) showed minor differences in relationships; however, median ages and 95% credibility intervals varied significantly between both analyses. The age of the last most common ancestor of Aphidoidea and Coccoidea (293 Ma [95% interval: 292, 299]), as well as the age of Coccoidea (226 Ma [95% interval: 202, 254]), did not differ significantly between analyses. In the total-evidence analysis, 21 fossils were included in Clade _a_ (Figure 5.7). By assessing differences among common nodes in this clade, of the eight nodes, three had younger ages when including fossils in the analyses, four had older ages, and the node defining Clade _a_ had the same age. In Clade _b_, 22 fossils were included in the total-evidence analysis; of the 16 common nodes assessed, deeper nodes were older with fossils incorporated, whereas the less inclusive nodes resulted in younger ages. Wood et al. (2013) recovered older ages on deeper nodes in total-evidence divergence estimates of
palpimanoid spiders, but incorporated fossils that only represented an isolated clade.

Ronquist et al. (2012a) retrieved nodes outside Hymenoptera that were much older (e.g., Carboniferous-aged), but with younger ages within Hymenoptera, when fossils across Hymenoptera were added to the analysis. In our study, fossils were also evenly distributed across the phylogeny of Coccoidea, and the deeper nodes were also pushed back significantly (into the Permian and Triassic), but because the age of the Coccoidea remained similar between both analyses, deeper branches were shorter in the total evidence topology.

Differences in 95% credibility intervals can also be affected by the incorporation of fossils. Fossils with highly incomplete dataset could increase this interval. However, in Pyron (2011), removing fossils that had the fewest characters (< 10%) did not lead to significant changes in median branch lengths, and the 95% credibility interval was greater, especially for clades where many fossils were removed. In our analyses, when assessing the 26 common nodes between the node-calibrated and total evidence approaches, the 95% credibility interval was nearly equivalent for the split between Aphidoidea and Coccoidea. However, all other nodes had significantly narrower 95% credibility intervals when fossils were incorporated in the analysis. Diverse, well-preserved fossils – such as is the situation for the Coccoidea -- improve not just time estimates, but error ranges as well. In general, the addition of fossil taxa also seems to overcome the drawback of missing data, by providing additional temporal information that reduced the absolute range of the 95% confidence interval.

Morphological characters in this analysis are driving the divergence time estimates. This assumes a certain rate of evolution for this type of data, which still retain
theoretical and implemental issues. The main issue resides in the estimation of rates of change for morphological characters (Pyron, 2011). Despite this significant conundrum, we have found that simply using node-calibration for divergence time estimates limits the use of fossil information, especially in Coccoidea where there are numerous fossils that cannot be placed with certainty unless a phylogenetic analysis is pursued. Such fossils could not simply be applied to a phylogeny post facto. Among the 43 fossils sampled, only 13 could be classified into Recent families with confidence. In general, before attempting to improve the sophistication of models for morphological evolution, incorporating fossils in a total-evidence framework still provides sufficient advantages compared to only using them as temporal information. This is particularly true for lineages where known past diversity is large but not represented today.

*The Borchsenius (1958) and Koteja (2001) hypotheses*

The two major hypotheses of coccoid phylogeny (i.e., phylogenetic relationships over geological time) were by Borchsenius (1958) and Koteja (2001: fig. 3) (the latter also updated and summarized in Grimaldi and Engel, 2005). Borchsenius (1958) provided a tree of scale insect evolution on a geological scale, basing the ages on geographical and host plant distributions of Recent coccoids. On these evidences only (fossil knowledge in Coccoidea was still lacking), he suggested that all extant families were established *before* the Cretaceous, pushing the origin of Coccoidea back to the Carboniferous. Koteja (2001) translated and reproduced Borchsenius’s tree (1958), noting errors (e.g., that the Permian was omitted and the Carboniferous placed adjacent to the Triassic). If Borchsenius had actually hypothesized a coccoid origin in the Permian, our divergence time estimates of the origin of Coccoidea in the Triassic are close to his.
suggestion. By hypothesizing such as old divergence, he further postulated that
vicariance must have been the main driver for explaining Recent distribution of tis
superfamily. In context, though, and as Koteja (2001) pointed out, Borchsenius (1958)
was writing before any pre-Tertiary Coccoidea were known (even the Baltic amber
fossils were poorly studied), and continental drift – let alone its possible effects on animal
and plant distributions – was still controversial (Grimaldi and Engel, 2005).

Koteja was a visionary, who applied his morphological acumen to fossils in an
attempt to elucidate scale insect evolution. His only tree of Recent and fossil families
(Koteja, 2001: Fig. 3), though drawn by hand, was based on 30 years of intensive study.
At the time, he had already studied some Cretaceous coccoids in Burmese and Lebanese
amber, though had not yet published them. Koteja divided the archaeococcoids into three
main “branches” (i.e., groupings). The first one included the Ortheziidae, Matsucoccidae
and Xylococcidae; the second the Monophlebidae and Margarodidae; and the third
Steingeliidae and Pityococcidae. Our results are quite similar: Clade a1 (Figure 5.7)
includes the Matsucoccidae and Ortheziidae, but not the Xylococcidae; Clade a2 includes
the Margarodidae, Monophlebidae and Xylococcidae; and finally, the Steingeliidae and
Pityococcidae are found in less inclusive nodes, closer to the neococcoids. Although,
Koteja did not assess relationships among the Recent families of each branch, he
tentatively placed fossil groups branching out of or near these families. An Early
Cretaceous ortheziid in Lebanese amber, for example, subsequently described as
Cretorthezia (Koteja and Azar, 2008), is retrieved in our analysis as the sister group to
the rest of the Ortheziidae, suggesting an origin of the family at 162 Ma [95% interval:
135, 193]. The family Jersicoccidae, in Late Cretaceous New Jersey amber (Koteja,
2000) was hypothesized to be related to the Monophlebidae in Koteja (2001). Our analysis confirms this relationship, with Jersicoccidae forming a clade with another Cretaceous family (the Hodgsonicoccidae, in Lebanese amber), together sister to the Recent Coelostomidiidae and Monophlebidae. The family Grimaldiellidae, also described in New Jersey amber (Koteja, 2000a), was placed by Koteja as branching out of the Margarodidae. Although he considered this family in a broader sense, our results confirmed that the Grimaldiellidae is an extinct sister group to the Margarodidae *sensu stricto*. Koteja’s “branch III” includes those families with eyes comprised of multiple but simple, isolated facets, which are also the groups forming successive sister groups to the neococcoids and forming Clade *b* in Figure 5.7. These correspond to the “polyphyletic unit grouping advanced forms of derived archaeococcoids” (Koteja, 2001: 51). Although, he put the Putoidae in the neococcoids, he still considered “*Puto* was the ancestor of all neococcids which are then monophyletic” (Koteja, 2001: 48). In other words, Putoidae is the sister group to all neococcoids, as is confirmed here. Koteja concludes by suggesting the origin of scale insects during the Triassic, which is corroborated by our results.

*Diversification of the neococcoids compared to the angiosperms and ant evolution*

Model-based estimates of divergence times must be interpreted prudently. This is particularly the case in studies where fossils are scarce and/or poorly preserved, a problem largely circumvented with Coccoidea given their diversity and excellent preservation in amber from 125 to 20 Ma. However, an absence of Jurassic and Triassic Coccoidea provides less confidence in the timing of their basal divergences. Secondly, divergence times can appear misleadingly precise, and because confidence intervals are often greater than the durations of the lineages, aspects of these studies that have been
roundly critiqued (Graur and Martin, 2004). Lastly, a very common problem in studies of
divergence time is the fallacy of “hypothesis stacking” which should be avoided. This is
the situation where a hypothesis of phylogenetic relationships layered with estimates of
divergence times is then used as direct evidence for comparisons to other divergence time
hypotheses or geological events, such as angiosperm radiations or continental drift. We
make an appeal that such comparison not be divorced from, especially not contradict, the
real direct evidence, namely that of accurately placed fossils along with rigorous practice
leading to divergence time estimates (Parham et al., 2012). A good example of this
regards two estimates of Cretaceous angiosperm lineages, by Crepet et al. (2004), and by
Magallón and Castillo (2009). The study by Crepet et al. (2004) estimated the major
angiosperm radiations at 113-80 Ma using the morphology of carefully selected
Cretaceous fossils and Recent exemplars; that of Magallón and Castillo (2009) estimated
this radiation at 130-100 Ma based on a node-calibration approach using molecular data.

The view that the neococcoid scale insects are largely a Tertiary radiation
(Grimaldi and Engel, 2005) needs to be revised. Three mid- to Early Cretaceous
neococcoids (Rosahendersona, Pennygallania, and Inka), albeit rare in the Cretaceous,
were significantly diversified by then. This is further supported by the finding that
Eopseudococcus and Geropseudococcus are Cretaceous sister groups to the mealybugs
(Pseudococcidae). While the Cretaceous angiosperm radiations probably had little effect
on the family-level origin of coccoids, it is quite possible that diversification within some
scale insect families was affected, and studies including a larger taxonomic need to be
undertaken. Coccoidea are without question an ancient group that is probably Triassic in
origin and largely radiated on gymnosperms; during and after the Cretaceous, this major phytophagous lineage shifted onto angiosperms.

Another pivotal group with which scale insects interact, besides angiosperms, are the ants (reviewed in Hölldobler and Wilson [1991]). Ants harvest honeydew from a variety of hemipterans, but some of their most intimate symbioses are between mealybugs and various dolichoderine ants. Wilson (Wilson and Hölldobler, 2005) even suggested that this interaction, trophobiosis, partly fostered the “dynastic succession” of ants, from primitive groups with small colonies to the subfamilies living in large colonies that are so ecologically dominant today. Fortunately, ants are well studied phylogenetically and there is a significant number of Cretaceous fossils in amber, the oldest of which is from the Early Cretaceous (ca. 105 Ma) from France (review in LaPolla et al., 2013); the oldest formicine (another major subfamily that harvests honeydew) is 90 Ma (Grimaldi and Agosti, 2000), and the oldest dolichoderine 78 Ma (McKellar et al., 2013). It is estimated on the basis of morphology that ants originated in the Early Cretaceous ca. 120 Ma (Grimaldi and Agosti, 2000), or as early as the Late Jurassic based on node-calibrated molecular estimates (Moreau et al., 2006), although the latter estimate exceeds the age of the oldest fossil aculeates, the inclusive group of wasps to which ants belong. As for angiosperms, coccoids well preceded ants, though it is possible that ants have had evolutionary effects on certain families of coccoids, such as pseudococcids.

Conclusions

This study provides an interfamilial phylogenetic assessment of Coccoidea using molecular data as well as morphological characters of adult females and males, and
incorporating 30% of fossil taxa. We inferred divergence time estimates integrating these fossils as terminals. Our results support the hypothesis of Borchsenius (1958) that scale insects originated before the Jurassic and, by the Early Cretaceous, most families were already established. Despite the large amount of missing data caused by both fossil and recent taxa for which only morphological characters were available, this study highlights the importance of fossil taxa and that should be an integral part of a divergence time estimates analysis. In this goal, making the morphological matrix available on online platforms such as Morphobank (O’Leary and Kaufman, 2011) will potentially allow future investigators to complete morphological coding and provide a more complete taxon sampling. Additionally, as more and more paleontological studies are integrated in phylogenetic studies, it appears critical to augment and have morphological characters as accessible as possible as it is already the case for DNA sequence data (Pyron, 2011).
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CHAPTER VI

CONCLUSIONS

This dissertation aimed at reconciling neontology and paleontology in an important plant-pest insect superfamily. As such, each chapter is presented in a logical order in the purpose of incorporating fossil taxa into a scale insect phylogenetic framework and obtaining divergence time estimates of their main lineages. This work will hopefully contribute towards answering further questions on Coccoidea evolution.

Here are the main concluding remarks emanating from this dissertation:

• Using the morphology of adult females, the phylogenetic assessment of the family Ortheziidae incorporates fossil taxa from amber deposits ranging over 100 My for the first time. This phylogeny supports the classification of Kozár. However, this scale insect family is exceptional in having fossilized female stages as opposed to the majority of Coccoidea fossil inclusions that are macropterous males.

• Descriptions of seven Ortheziidae macropterous males increase our knowledge of male morphology from 5 to 12 morphogroups. The generic classification defined by Kozár based on adult female morphology is supported. In the future, similar studies of both male and female morphology must become an important part of scale insect systematics.

• A total of 21 new species, 14 new genera and three new families of fossil scale insects are described in ambers ranging from the Early Cretaceous to the Miocene. A significant Early Cretaceous diversity is uncovered with more
specialized archaeococcoid extinct groups. Important first records include new members of the Margarodidae and Diaspididae from Indian amber and a new Coccidae genus from Early Cretaceous Burmese amber, the latter discovery pushes back the origin of this family and the neococcoid lineage.

- Finally, by sampling 73 Recent and 43 extinct taxa from 48 families, I provide a phylogenetic hypothesis across the Coccoidea and estimate the first divergence times of the main lineages using both molecular sequences and morphological characters from adult males and females. The origin of the Coccoidea is estimated at around 220 Ma, during the Late Triassic, and suggests that of the appearance of the hyperdiverse neococcoids was almost 100 million years prior to the diversification of angiosperms in the mid-Cretaceous.

- Despite the incomplete data for fossil coccoids, partly because of the lack of female morphological characters, their use for both temporal and morphological information appears to be more and more beneficial and soon critical in providing timescales for phylogenetic hypotheses.

This dissertation constitutes a preliminary evaluation of fossil use in a phylogenetic context for scale insects. To further advance the evolutionary understanding in Coccoidea, the following are suggested:

1. **A steady exploration for adult male morphology of disparate taxa appears necessary.** This would not only provide a rich source for informative systematic characters, but will be essential for a more thorough interpretation of fossilized males. Both the collection (by describing other undescribed specimen in major
scale insect collections) and by field exploration through networking with coccoid specialists on various continents would fill the gap of morphological knowledge between males and females. Provided that the female is already known, barcoding would provide positive association between male and females.

2. **Continued and even expanded screening, preparation, and study of coccoid inclusions in various ambers around the world will allow a revised and refined interpretation of the coccoid fossil record.** Even though Baltic amber was the focus of intense study by Jan Koteja, new taxa from that deposit continue to be discovered. The 52 Myo Cambay amber from western India shows exceptional promise. It is a prolific deposit and, with only a few of the coccoid inclusions studied at this point, including the first fossil Margarodidae (Chapter IV). Amber of a similar age from the Paris Basin, Oise, France, is also potentially important. With the discovery that neococcoids existed well into the Cretaceous, the exploration of Cretaceous amber is most important. There are still many more coccoid inclusions awaiting meticulous preparation in collections of 100 Myo Burmese and 90 Myo New Jersey ambers, undoubtedly with a significant diversity of new taxa. It is unclear why Canadian, French, Siberian, and Spanish Cretaceous amber contain so few (or no) coccoid inclusions, but undescribed inclusions in these deposits still require study, as do all coccoids in some of the newly discovered Cretaceous deposits (e.g., from Alabama and Ethiopia). Given the antiquity of Coccoidea, and even the neococcoids, the Early Cretaceous Lebanese amber has primary significance. With the recent discovery of small
arthropod inclusions in Late Triassic amber, a coccoid in this amber would be an exceptional discovery.

3. **Definition of new molecular markers, especially protein-coding genes.** Despite the common use of DNA sequence data for phylogenetic analyses, such sequences are still limited for scale insects. Generating genomic data for representatives in major families would potentially provide understanding on how genes evolved across Coccoidea and why consistent genetic markers for use across the superfamily are not established yet.

4. **Consideration of developmental biology in a phylogenetic context** could provide better understanding on the evolution of intriguing and phylogenetically significant characters, such as the diversity of eye types and genitalia in macropterous adult males.
APPENDIX A

SUPPLEMENTARY MATERIAL FOR CHAPTER II
Table S2.1. Data matrix for sampled Ortheziidae and outgroups. See results section for a description of characters and character states and Figs 2.2-2.12 for images of character states.

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Figure S2.1. Analysis without *Acorygorthezia williamsi*. Strict consensus of 12 most parsimonious trees recovered with the Traditional search in TNT. L=281, CI=0.3, RI=0.67.
APPENDIX B

SUPPLEMENTARY MATERIAL FOR CHAPTER IV
Table S4.1. List of taxa used on the morphological analysis, see Table 4.2 for fossil deposits

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Table S4.2. Data matrix for sampled Coccoidea and outgroups. See results section for descriptions of characters and character states.

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Conchaspisa
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Crypticerya
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Magnaelentis
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Pedicelloccus
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00020?????00000011121322?1030002101?3020??1?3002?0?????0302?

ARC60.1
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APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER V
**Table S5.1. Information related to the molecular regions used in this study**

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<th>Type of character</th>
<th>Primer F</th>
<th>Primer R</th>
<th>Reference</th>
<th>Number of characters (after alignment)</th>
<th>Parsimony informative characters</th>
<th>Taxa coverage (% of 80 Recent taxa total)</th>
<th>Best-fitting model (BIC)</th>
<th>Model used in MrBayes</th>
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<td>TCG GAA GGA ACC AGC TAC TA</td>
<td>Morse &amp; Normark, 2006</td>
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<td>1138</td>
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**Models partition per codon**

- **EF-1a codon3**
  - TIM3+I
  - GTR+I
  - GTR+G

- **EF-1a codon12**
  - TPM2+I+G
  - GTR+I+G
  - GTR+G
Table S5.2: Node calibrations used for the calibrated MrBayes analysis

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<th>Fossil deposit</th>
<th>Age (Ma)</th>
<th>Parameter in MrBayes</th>
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<td>matsucoccidae=offsetexp(135,0.01538)</td>
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<td>Ortheziidae</td>
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<td>Lebanese (Cretorthezia)</td>
<td>135 (oldest estimate for node 200)</td>
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<td>Indian (TAD139)</td>
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<td>Burmese (BU835)</td>
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<td>Triassic stem aphidoid</td>
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Calibrations were set in MrBayes as a offset exponential distribution.

In order to determine the values of the command, the first value is the age and the second is 1/x with x being the difference between the age I set on first value and an older estimate. For example, for the Matsucoccidae, I used 135Ma for the fossil evidence, with an older estimation of the node back to 200Ma, so 200-135=65 and 1/65=0.01538. In the end the calibration for Matsucoccidae node will be offsetexp(135,0.01538). The variance is very subjective… we can try to narrow the variance of the distribution but for example, the earliest Margarodidae ss is found in 50Ma, and I think that the node shou ld be older, so I increase the variance.
### Table S5.3: Percentage of completeness of each terminal for different data categories

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<th>Morphology female</th>
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Figure S5.1: All compatibility tree resulted from Bayesian analysis of all extant taxa with both morphological and molecular data.
Figure S5.2: Strict clock analysis, majority rule tree
Figure S5.3: Branch length variance between non clock and strict clock topologies
APPENDIX D

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Isabelle M. Vea – Curriculum Vitae

Education

  - Advisor: David Grimaldi
  - Dissertation title: A time scale for scales: reconciling neontology and paleontology in Coccoidea (Hemiptera)
- **2006 – 2008. “Master” (equivalent to MS) in Systematic, Evolution and Paleontology**, Université Pierre et Marie Curie (UPMC) in partnership with the Muséum National d'Histoire Naturelle de Paris (MNHN), France
- **2003 – 2006. Licence (Equivalent to BSc.) in Life Sciences**, Université Pierre et Marie Curie, Paris, France

Employment and research internships

- **07/2008 – 09/2008** *Research intern, University of Massachusetts Amherst*, Department of Plants, Soil and Insects, Amherst, MA. Examined the morphological variation of *Chionaspis* species complex (Diaspididae) feeding on pine in North America and described four new species.
- **02/2008 – 06/2008** *Research intern, European Biological Control Laboratory (ARS-USDA)*, Monptellier, France. Tested molecular markers for collection specimens of *Eriococcus* (Eriococcidae)
Education training

07/2008  Phylogenetic workshop, The Willi Hennig Society, Ohio State University, Columbus, OH

09/2006  European Summer university on the Origin of Life and Life in space, Université Pierre et Marie Curie, Banyuls-sur-mer research station, France

2002-2003  Chinese Language Program, Beijing Language, University, Beijing, China.

Fieldwork and collection visits

05/2013  Florida, collecting trip.

06/2012  Silesia University, Katowice, Poland, scale insect amber collection.


05/2011  Natural History Museum, Entomology collections, London, UK.

01/2011  Biological Station of Los Tuxtlas, UNAM, Veracruz, Mexico.

09/2010  Southern Research Station, Portal AZ, collecting trip


Publications


**Conference Presentations**

• **November 2013**: 61st Annual meeting of the Entomological Society of America. Oral presentation: Towards a time scale for scales: divergence time estimation of major lineages in Coccoidea (Hemiptera).

• **August 2012**: 24th International Congress of Entomology. Preliminary phylogeny of early lineages of scale insects (Hemiptera: Coccoidea) based on adult male morphology from the early Cretaceous to Recent.

• **December 2010**: 58th Annual meeting of the Entomological Society of America. Poster: A morphological analysis of the Ortheziidae scale insects (Hemiptera: Coccoidea) including 100 million years of fossils in amber.

• **September 2010**: Second Annual Richard Gilder Graduate School Symposium. Oral presentation: A morphological analysis of the Ortheziidae scale insects (Hemiptera: Coccoidea) including 100 million years of fossils in amber.

• **April 2010**: 12th International Symposium of Scale Insect Studies. Poster: 145 million years of Ortheziidae.


**Awards and Grants**

2012: National Science Foundation Doctoral Dissertation Improvement Grant ($14,820)

2011: ESA SysEB Travel Grant for collection visit ($1,000)

2010: Theodore Roosevelt grant for fieldwork ($2,070)

2007-2008: Bourse du mérite ( Honour grant): 4000 EUR

December 2010: ESA Student Debate: Issues surrounding biodiversity - Winner of topic 3: “Transgenic insecticidal crops will conserve biodiversity”
Languages

- French: native
- English: fluent
- Chinese: advanced in speaking (intermediate in writing and reading)

Memberships

- Société Française de Systématique since 2007
- Entomological Society of America since 2010
- Willi Hennig Society since 2009

Volunteering


**Disclaimer taxon names in Chapter IV**

The names of new taxa described in Chapter IV of this dissertation do not constitute a nomenclatural act. For valid names, see Vea and Grimaldi (2015) published in Novitates. Some names have been changed between the publication of the dissertation and the article. The following table includes the list of corresponding names between the present dissertation and the Novitates article.

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