Diverse New Scale Insects (Hemiptera: Coccoidea) in Amber from the Cretaceous and Eocene with a Phylogenetic Framework for Fossil Coccoidea

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Diverse new scale insects (Hemiptera: Coccoidea) in amber from the Cretaceous and Eocene with a phylogenetic framework for fossil Coccoidea

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ABSTRACT

Coccoids are abundant and diverse in most amber deposits around the world, but largely as macropterous males. Based on a study of male coccoids in Lebanese amber (Early Cretaceous), Burmese amber (Albian-Cenomanian), Cambay amber from western India (Early Eocene), and Baltic amber (mid-Eocene), 16 new species, 11 new genera, and three new families are added to the coccoid fossil record: Apticoccidae, 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 patefactus,* n. gen., n. sp.; Kozariidae, n. fam., including *Kozarius achronus,* n. gen., n. sp., and *K. perpetuus,* n. sp.; the first occurrence of a Coccidae in Burmese amber, *Rosahendersonia prisca,* n. gen., n. sp.; the first fossil record of a Margarodidae *sensu stricto*, *Heteromargarodes hukamsinghi,* n. sp.; a peculiar Diaspididae in Indian amber, *Normarkicoccus cambayae,* n. gen., n. sp.; a Pityococcidae from Baltic amber, *Pityococcus moniliformalis,* n. sp., two Pseudococcidae in Lebanese and Burmese ambers, *Williamsicoccus megalops,* n. gen., n. sp., and *Gilderius eukrinops,* n. gen., n. sp.; an Early Cretaceous Weitschatidae, *Pseudoweitschatus audebertis,* n. gen., n. sp.; four genera considered incertae sedis, *Alacrena peculiaris,* n. gen., n. sp., *Magnilens glaesaria,* n. gen., n. sp., and *Pedicellicoccus marginatus,* n. gen., n. sp., and *Xiphos vani,* n. gen., n. sp. Interpretation of fossil coccoids is supported by a parsimony phylogenetic analysis based on 174 morphological characters (both adult males and females) and 112 taxa (69 Recent and 43 extinct).

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INTRODUCTION

The superfamily Coccoidea (based here on the classifications of, e.g., Gullan and Cook, 2007, and Hodgson and Hardy, 2013) 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 7900 Recent described species classified in 1110 genera and 33 Recent and 16 extinct 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? An approach we use here is to directly examine the evolutionary history of Coccoidea, which will be used later for divergence time analyses compared to those for angiosperms (Vea and Grimaldi, unpubl.).

The wingless, sedentary adult females and the nymphs represent the more conspicuous and long-lasting life-history stages, because during these stages they feed either exposed on the surface of their host plants or concealed (in internodes, under bark, and the like). This is why, despite highly reduced and specialized morphology, the taxonomy of Coccoidea is essentially based on the adult females (see Hardy, 2013, for a review). This stage, however, is 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.

Adult males are usually winged (rarely apterous), minute, 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). They are an excellent insect group for studying evolutionary changes over the past 130 million years, this being the onset of deposits of highly fossiliferous amber (Grimaldi and Engel, 2005) and encompassing the period of angiosperm radiations. Adult males are far less reduced in morphology than are the females, possessing long, multisegmented antennae; eyes (either fully compound, or with isolated facets); a pair of mesothoracic wings; well-developed legs, and simplified (Theron, 1958) yet diverse genitalia (Hodgson and Foldi, 2006). 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 informative morphology of adult males, comparative studies are few in contrast to their female counterparts (Afifi, 1968; Ghauri, 1962; Giliomee, 1967; Hodgson et al., 2007; Koteja, 1986a; Hodgson and Foldi, 2006; Theron, 1958; Vea, 2014). Nevertheless, sufficient comparative information exists among families and genera of some families, which potentially allows phylogenetic placement of fossilized males (Hodgson and Hardy, 2013).

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, *Eomatsucoccus andrewi* Koteja, 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 exclusively 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 two Eocene ambers. These descriptions are supported by a morphological phylogenetic analysis, based on 174 characters defined from both adult females and males, and comprising a total of 112 representatives (64 Recent and 43 fossils) of 44 Coccoidea families (including three new families herein described).

Historical Context

Early Workers: Our knowledge of the diversity and systematics of Coccoidea in the fossil record is actually quite good compared to that of most other insect groups, due almost exclusively to the contributions of 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 20th century (Cockerell, 1906; Cockerell, 1909). Prior to this, there were only isolated descriptions of fossil coccoids by 19th-century Germans who worked and published extensively on myriad organisms preserved in Baltic amber (Germar and Berendt, 1856; Koch, 1857). T.D.A. Cockerell (1866–1948) was a natural history polymath who published more than 3000 papers on bees (he described some 5400 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 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 *Dactylopius opuntiae* (Cockerell, 1896) (Dactylopiidae), a devastating, introduced pest of *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 C.L. Koch, G.K. Berendt, and E.F. Germar. However, Beardsley (1969) then described a species in Late Cretaceous (Santonian-aged) amber from Manitoba, Canada, *Electrococcus canadensis* Beardsley, 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 1980s, there was a burgeoning of studies on fossil coccoids, almost all of them by Koteja (see review in Koteja, 2000a).

Jan Koteja: Jan Koteja (1932–2004) was a highly talented authority on coccoids at Cracow Agricultural University, Cracow, 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: 302) in preparing meticulous dissections and amber preparations, highly detailed drawings, and his own catalog system for some of the 1700 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 paleoentomological papers provided descriptions of fossil Matsucoccidae (Koteja, 1984; Koteja, 1986b; Koteja, 1988a; Koteja, 1999) followed by studies of nymphal and adult males of Eriococcidae and related groups (Koteja, 1988b; 1988c). He published on Baltic amber fossils of the Ortheziidae, including adult males (Koteja, 1987a; 1987b) as well as adult females (Koteja and Żak-Ogaza, 1988a; 1988b). 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 among entomologists 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, in fact, was discovered as early as the 1930s (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 and Wolfe, 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 seven genera and 10 species, placed into seven families (table 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. 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 1 mm 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 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 1970s (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 general 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 Ukraine is similar in age to Eocene Baltic amber and chemically identical, although it contains species and genera not present in Baltic amber (Perkovsky et al., 2007). Recent study of a composition containing Diptera species in Rovno amber suggests that it could be the same as Bitterfield amber (Szwedo and Sontag, 2013). 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 significantly distinct from that in Baltic amber. Late Albian amber from Alava, northern Spain (Alonso et al., 2000; Peñalver and Delclòs, 2010) Basque-Cantabrian Basin, 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 Amber Deposits below) 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).

Materials and Methods

Amber Deposits: The Coccoidea fossils studied here were derived from four deposits, two of them Eocene, the other two Cretaceous. One of the two Eocene 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 Eocene deposit involves Cambay amber from western India. This material was excavated directly by one of us (D.A.G.), 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 thus 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 highly cross-linked and polymerized). Thus, some inclusions can be extracted from Cambay amber (see Rust et al., 2010: fig. 1B, C), 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 Canada balsam and/or epoxy embedding. This deposit has already yielded a high diversity of Coccoidea (Koteja and Azar, 2008), and new specimens are still regularly found (Azar, personal commun.).

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 emery 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 100–400×. Because of the minute size of many specimens and the high magnifications required, many amber pieces were trimmed and polished to ca. 2 × 2 × 1 mm. In such cases, final grinding and polishing was done by hand, gently pressing the minute amber chip against the surface of wet emery 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 microscope; details were added using direct observation through this microscope at various focal planes, as well as with a Leitz Wetzlar stereoscope at magnifications up to 144×. Measurements were made using ImageJ vers. 1.46R (Abramoff et al., 2004). 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 40–100× 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 ZP (Hadley, 2010).

Morphological terminology follows previous work by Hodgson and Foldi (2006) except for wing morphology where Koteja's terminology was used (e.g., Koteja, 2000b; 2004; 2008).

Material is deposited in the following repositories: AMNH, Division of Invertebrate Zoology, American Museum of Natural History, New York, New York, (Burmese and some Lebanese amber specimens); BSIP, Birbal Sahni Institute of Palaeobotany, Lucknow, India (holotypes of Cambay amber); and MNHN, Paris Museum National d'Histoire Naturelle in Paris (Dany Azar collection).

ABBREVIATIONS FOR MORPHOLOGICAL STRUCTURES IN PHOTOMICROGRAPHS

These are based on Hodgson and Foldi (2006) for body structure terminology and on Koteja's (2000b; 2004; 2008) work for wing morphology.

abd	abdomen
abds	abdominal setae
ae	aedeagus
afp	anterior flexing patch
aln	alar notch
br	bristle
bs	basisternum
ce	compound eye
cl	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
prnr	pronotal ridge
prsc	prescutum
prtx	prothorax
ps	penial sheath
pt	pterostigma
sc	scape
scr	subcostal ridge
sctl	scutellum
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: Terminals of 107 ingroups (Coccoidea) and five outgroups (Aphidoidea) were selected for the analysis. The total ingroup taxon sampling included 72 Recent species and 43 fossil species, representing 41 of the 49 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 the appendix.

MORPHOLOGICAL CHARACTERS: One hundred and seventy-four morphological characters were defined and include 124 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, in the AMNH and MNHN for amber inclusions, or the literature (see appendix).

ADULT MALE MORPHOLOGY

Head

1. Functional mouthparts: 0 = present; 1 = absent.
2. Genae: 0 = absent; 1 = present with setae; 2 = present without setae.
3. Pores on head: 0 = absent; 1 = present.

4. Dorsal median crest: 0 = absent; 1 = present.
5. Extension of dorsal midcranial ridge: 0 = extends across head and touches postoccipital suture; 1 = extends to half-length of head but does not extend to postoccipital suture; 2 = very short; 3 = absent.
6. Dorsomedial part of epicranium: 0 = reticulated; 1 = not reticulated.
7. Postoccipital suture: 0 = absent or reduced; 1 = symmetrical Y shape; 2 = asymmetrical Y shape; 3 = curved; 4 = linear.
8. Postocular ridge: 0 = absent; 1 = present dorsally and ventrally; 2 = present only ventrally; 3 = present only dorsally.
9. Preoral ridges: 0 = absent; 1 = present.
10. Ventral midcranial ridge: 0 = short; 1 = extending to midlength of head; 2 = extending to posterior part of head; 3 = absent.
11. Ventral midcranial ridge setae: 0 = absent; 1 = present.
12. Ventral midcranial ridge fusion to other ridges: 0 = not fusing; 1 = fusing to preoral ridge; 2 = fusing to lateral preocular ridges.
13. Ventral preocular ridge: 0 = absent; 1 = present.
14. Ventral setae on head: 0 = present; 1 = absent.
15. Armed-cross ridges on ventral side: 0 = present; 1 = absent.
16. Satellite setae: 0 = present; 1 = absent.
17. Ocular sclerite setae: 0 = absent; 1 = present.

Eyes

18. Type of eyes: 0 = compound (complex eyes with many ommatidia, e.g., Ortheziidae, Matsucoccidae, Xylococcidae, Monophlebidae); 1 = simple (eyes composed of simple facets varying from two [e.g., Diaspididae] to eight pairs [e.g., Phenacoleachiidae]).
19. Relative location of eyes: 0 = dorsal and ventral eyes at same level; 1 = dorsal eyes anteriorly relative to ventral eyes; 2 = ventral eyes anteriorly relative to dorsal eyes; 3 = laterally.
20. Relative size of eyes: 0 = same size; 1 = dorsal bigger than ventral; 2 = ventral bigger than dorsal.
21. Number of eye units (ommatidia or eye facet): 0 = more than 100; 1 = between 51 and 100; 2 = between 9 and 50; 3 = 8 pairs; 4 = 7 pairs; 5 = 6 pairs; 6 = 5 pairs; 7 = 4 pairs; 8 = 2 pairs.
22. Number of rows of simple eyes: 0 = one; 1 = at least two; 2 = simple eyes absent.
23. Eyes joining ventrally: 0 = yes; 1 = no.
24. Larval eye persistent in adult stage (called ocellus in scale insect morphology): 0 = dorsally; 1 = laterally; 2 = absent.
25. True ocelli (organs found on the posterior part of the head in most insects and present in aphids): 0 = absent; 1 = present.

Antennae

26. Number of antennal segments: 0 = of aphid type; 1 = less than 10 segments; 2 = 10 segments; 3 = more than 10 segments.
27. Relative length of antennal setae: 1 = longer than antenna diameter; 2 = shorter than antenna diameter.

28. Reticulations on antennae: 0 = absent; 1 = present on pedicel only; 2 = on other antennal segments.
29. Antennal pedicel enlarged: 0 = no; 1 = yes.
30. Antennal fleshy setae: 0 = present; 1 = absent.
31. Antennal bristles: 0 = present; 1 = absent.
32. Antennal capitate setae: 0 = absent; 1 = present on apical setae only; 2 = present on other antennal segments.
33. Lateral extensions on antennal segments: 0 = present; 1 = absent.
34. Flagellomere structure: 0 = filiform (longer than wide and without obvious nodulation); 1 = with obvious nodulations on each segment; 2 = round (long as wide).
35. Type of nodulation on flagellomere: 0 = absent; 1 = trinodose; 2 = binodose.

Thorax

36. Neck constriction: 0 = absent but head and thorax distinct; 1 = strongly marked; 2 = slightly marked; 3 = head completely fused to thorax.
37. Prothorax: 0 = sclerotized; 1 = membranous.
38. 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.
39. Pronotal ridge: 0 = absent; 1 = curved, U-shaped; 2 = short; 3 = trilobed.
40. Prosternum: 0 = present as a ridge; 1 = absent; 2 = present as a sclerotized plate; 3 = prothorax completely sclerotized.
41. Prosternal transverse ridge: 0 = absent; 1 = present.
42. Prosternal setae: 0 = present; 1 = absent.
43. Posttergites. 0 = absent; 1 = present.
44. Triangular plates: 0 = absent; 1 = present.
45. Tegular setae: 0 = absent; 1 = present.
46. Mesoprephragma: 0 = absent; 1 = present.
47. Prescutum: 0 = nodulated; 1 = not nodulated; 2 = absent.
48. Shape of the prescutum: 0 = an inverted triangle; 1 = elongated, oval, oriented vertically; 2 = triangular, with round posterior ridge and separated medially; 3 = round; 4 = oval elongated horizontally; 5 = square.
49. Prescutal ridge: 0 = heavily sclerotized; 1 = lightly sclerotized; 2 = absent.
50. Prescutal suture: 0 = meet medially; 1 = do not meet medially; 2 = absent.
51. Prescutal setae: 0 = present; 1 = absent.
52. Prescutum and scutum: 0 = not distinctly separated; 1 = distinctly separated.
53. Oval membranous areas posterolaterally on prescutum: 0 = present; 1 = absent.
54. Scutum: 0 = absent; 1 = not nodulated; 2 = nodulated.
55. Scutal setae: 0 = absent; 1 = present.
56. Scutal pores: 0 = absent; 1 = present.
57. Oval membranous areas on scutum: 0 = oval; 1 = absent; 2 = quadrate; 3 = triangular; 4 = lateral areas.

58. 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.
59. Scutellar setae: 0 = present; 1 = absent.
60. Scutellar pores: 0 = present; 1 = absent.
61. Membranous area on scutellum: 0 = absent; 1 = on lateral side only; 2 = laterally and medially; 3 = only medially.
62. Foramen on scutellum: 0 = present; 1 = absent.
63. Marginal ridge on basisternum: 0 = absent; 1 = present and well sclerotized; 2 = present and poorly sclerotized.
64. Basisternum furca: 0 = base wide; 1 = base narrow; 2 = base intermediate in width.
65. 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.
66. Basisternum median ridge: 0 = strong; 1 = weakly sclerotized in parts; 2 = absent.
67. Basisternal setae: 0 = present; 1 = absent.
68. Length of mesopostnotum relative to combined mesothoracic structures (Mesoprescutum + mesoscutum + mesoscutellum): 0 = obviously longer; 1 = about the same length; 2 = shorter.
69. Mesopostnotal apophysis: 0 = well developed; 1 = reduced; 2 = absent.

Legs

70. Leg reticulations: 0 = absent; 1 = present.
71. Type of foreleg: 0 = walking (subequal to meso- and metalegs); 1 = fossorial (proleg significantly shorter and more stout).
72. Long flagellate seta on metatrochanter: 0 = absent; 1 = present.
73. Bifurcated setae on profemur: 0 = absent; 1 = present.
74. Number of tibial spurs: 0 = two; 1 = multiple; 2 = one; 3 = absent.
75. Type of tibial spurs: 0 = spinose; 1 = clavate; 2 = undifferentiated.
76. Number of tarsal segments: 0 = two well-developed tarsal segments; 1 = two tarsal segments with the one between tibia and tarsal segment 2 reduced; 2 = one tarsal segment.
77. Bifurcated setae on tarsus: 0 = present; 1 = absent.
78. Tarsal digitules: 0 = absent or hairlike (i.e., undifferentiated); 1 = present as one pair of thinly clavate digitules; 2 = present as more than one pair of thinly clavate digitules
79. Number of claws: 0 = one; 1 = two.
80. Number of claw digitules: 0 = two; 1 = more than two; 2 = absent.
81. Type of claw digitules: 0 = hairlike/setose; 1 = spinelike/spinose; 2 = broadly clavate; 3 = thinly clavate; 4 = absent.
82. Claw digitules protrude out of claw: 0 = no; 1 = yes.
83. Claw denticle: 0 = absent; 1 = present.

Forewings

84. Ratio of wing to antenna: 0 = wing longer than antenna; 1 = antenna longer than wing; 2 = subequal.

85. Base of forewing: 0 = narrow; 1 = broad.
86. Apex of forewing: 0 = round; 1 = pointed; 2 = bilobed.
87. Subcostal ridge: 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.
88. Ridges other than subcostal ridge cubital ridge: 0 = absent; 1 = present.
89. Length of cubital ridge: 0 = long (almost reaches margin); 1 = short (less than halfway to margin).
90. Origin of cubital ridge: 0 = originating on subcostal ridge, both ridges forming a Y shape; 1 = originating on wing base, forming a V shape.
91. Posterior flexing patch: 0 = absent; 1 = present.
92. Anterior flexing patch: 0 = absent; 1 = present.
93. Pterostigma: 0 = absent; 1 = present.
94. Forewing microtrichia: 0 = absent; 1 = present.
95. Alar setae: 0 = absent; 1 = present.
96. Alar sensoria: 0 = absent; 1 = present.
97. Structure attaching the hamuli to the forewing: 0 = absent; 1 = alar fold; 2 = alar lobe.

Hindwings

98. Hindwing: 0 = completely developed; 1 = leaf-shaped hamulohalteres; 2 = narrow elongated and parallel-sided hamulohalteres; 3 = absent.
99. Number of hamuli: 0 = absent; 1 = one; 2 = two or more.
100. Location of the hamuli: 0 = on the anterior ridge of the hind wing; 1 = at the tip of the hind wing.

Abdomen

101. Abdominal dorsal setae: 0 = absent; 1 = present; 2 = very few.
102. Abdominal dorsal pores: 0 = absent; 1 = present.
103. Abdominal pleural setae: 0 = absent; 1 = present; 2 = very few.
104. Abdominal pleural pores: 0 = absent; 1 = present.
105. Abdominal ventral setae: 0 = absent; 1 = present; 2 = very few.
106. Abdominal ventral pores: 0 = absent; 1 = present.
107. Abdominal caudal extension: 0 = abdominal segments V to VIII; 1 = abdominal segment VIII only; 2 = absent.
108. Relative length of caudal extensions: 0 = subequal; 1 = increasing in size posteriorly; 2 = one pair of caudal extension; 3 = absent.
109. Cornicles on abdominal segment VII: 0 = present; 1 = absent; 2 = modified into ostioles.
110. Tubular ducts: 0 = present on tergites VI and VII; 1 = present on tergite VII only; 2 = present on tergite VI only; 3 = absent.
111. Rows of tubular ducts on each abdominal segment: 0 = one; 1 = more than one; 2 = no tubular ducts.
112. Glandular pouches producing pairs of wax tails on last abdominal segments: 0 = absent; 1 = on abdominal segment VIII only; 2 = on abdominal segment VII and VIII.

113. Type of glandular pouch (adapted from Hodgson and Hardy [2013]): 0 = group of pores but not pouchlike and flat (e.g., *Phenacoleachia*); 1 = shallow pouch (e.g., *Puto, Steingelia*); 2 = deep pouch (e.g., Pseudococcidae, Eriococcidae, Coccidae); 3 = absent.
114. Glandular pouch setae (extending out from glandular pouch): 0 = no setae with glandular pouch; 1 = one pair; 2 = two pairs; 3 = three pairs; 4 = more than three pairs.
115. Longer setae on abdominal segment VII (other than those associated to glandular pouch): 0 = absent; 1 = one pair; 2 = two pairs; 3 = more than two pairs.
116. Abdominal spiracles: 0 = absent; 1 = very obvious, well developed; 2 = obscure, but possibly present and very small (evidenced by the presence of tracheae).
117. Abdominal spiracle distribution: 0 = all are present (8); 1 = more than half; 2 = less than half; 3 = absent.

Genital segments

118. Penial sheath: 0 = triangular; 1 = quadrate; 2 = spinelike; 3 = oval; 4 = rhomboid.
119. Penial sheath position: 0 = ventrally and more anterior relative to anus location on dorsum; 1 = ventrally but more posterior relative to anus location on dorsum; 2 = protruding out of abdomen.
120. Penial sheath setae: 0 = absent; 1 = abundant; 2 = very few.
121. Relative size of the penial sheath (length divided by base width): 0 = inferior to 1; 1 = between 1 and 5; 2 = between 5.1 and 10; 3 = more than 10.
122. Penial sheath apically bifurcated: 0 = yes; 1 = no.
123. Basal rod on aedeagus: 0 = absent; 1 = present.
124. Endophallus: 0 = present; 1 = absent.

Adult Female Morphology

Head

125. Labium segmentation: 0 = one segment; 1 = two segments; 2 = three segments; 3 = four segments; 4 = mouth absent.
126. Eye location: 0 = margin; 1 = dorsum; 2 = venter; 3 = eye absent.
127. Reticulations of antennae: 0 = absent; 1 = on pedicel only; 2 = on other antennal segments.

Antennae

128. Number of antennal segments: 0 = less than 5; 1 = 5 or 6; 2 = 7; 3 = 8 or more; 4 = antenna absent.
129. Type of flagellomeres: 0 = round; 1 = filiform but all subequal; 2 = filiform but with length differences; 3 = wider than segment length.

Legs

130. Legs: 0 = absent; 1 = present but reduced; 2 = fully developed.
131. Type of legs: 0 = all walking; 1 = fossorial; 2 = metathoracic developed and pro- and mesothoracic legs reduced; 3 = absent.
132. Reticulations on legs: 0 = absent; 1 = present.
133. Long setae on trochanter: 0 = absent; 1 = present.

134. Shape of trochanter: 0 = small and rectangular (Ortheziidae); 1 = triangular but one side round and overlapping femur; 2 = triangular (Pseudococcidae); 3 = absent.
135. Trochanter and femur: 0 = fused; 1 = unfused; 2 = absent.
136. Tibia and tarsus: 0 = fused; 1 = unfused; 2 = absent.
137. Tibiotarsal articulation: 0 = absent; 1 = present; 2 = absent.
138. Relative length of tibia and tarsus: 0 = tibia longer than tarsus; 1 = tarsus longer than tibia; 2 = tibia and tarsus of subequal length; 3 = absent.
139. Number of tarsal segments: 0 = one; 1 = two; 2 = absent.
140. Number of claw digitules: 0 = two; 1 = more than two; 2 = absent; 3 = absent.
141. Claw digitules: 0 = shorter than claw; 1 = longer than claw; 2 = absent.
142. Claw denticle. 0 = absent; 1 = present; 2 = absent.

Abdomen

143. Abdominal crenulations: 0 = absent; 1 = present.
144. Abdominal spiracles: 0 = absent; 1 = between one and four; 2 = more than four.
145. Circulus: 0 = absent; 1 = present.
146.Cerarii: 0 = absent; 1 = present on all segments; 2 = present on last abdominal segments only.
147. Ostioles: 0 = absent; 1 = present anteriorly and posteriorly; 2 = just posterior, as cornicles.
148. Cribriform plates: 0 = absent; 1 = present.
149. Ovisac band: 0 = absent; 1 = present.
150. Pygidium: 0 = absent; 1 = present.
151. Anal plates: 0 = absent; 1 = one anal plate; 2 = two anal plates.
152. Anal lobes: 0 = absent; 1 = present.
153. Anal cleft: 0 = absent; 1 = present.
154. Anal ring: 0 = absent; 1 = present with setae; 2 = present without setae.
155. Body pores: pores around abdominal spiracles: 0 = absent; 1 = present.
156. Pores on atrium of thoracic spiracles: 0 = absent; 1 = present.
157. Pores in peritreme of abdominal spiracles: 0 = absent; 1 = present.
158. Bilocular pores: 0 = absent; 1 = present.
159. Perivulvar pores: 0 = absent; 1 = present.
160. Perispiracular pores: 0 = absent; 1 = present.
161. Pores on anal ring: 0 = absent; 1 = present.
162. 8-shaped pores: 0 = absent; 1 = present.
163. Trilocular pores: 0 = absent; 1 = present.
164. Quadrilocular pores: 0 = absent; 1 = present.
165. Tubular ducts: 0 = absent; 1 = present.
166. Multilocular pores with more than 6 loculi: 0 = absent; 1 = present.
167. Quinquelocular pores: 0 = absent; 1 = present.

Body setae

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

169. Setae on dorsum: 0 = absent; 1 = present; 2 = very few.
170. Setae on venter: 0 = absent; 1 = present; 2 = very few.
171. Spiracular setae: 0 = undifferentiated from marginal setae; 1 = differentiated.
172. Dermal papillae: 0 = absent; 1 = present.

General

173. 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.
174. Type of oviposition: 0 = within ovisac; 1 = under a protective cover; 2 = external to female body; 3 = internal marsupium.

Parsimony Analysis: The morphological matrix was analyzed using maximum parsimony (MP) as the optimality criterion, implemented in TNT (Goloboff et al., 2008). The search was performed as follows: *Acyrthosiphon* (Aphidoidea) was defined as the outgroup (command line: out acyr;), all characters were treated as unordered, except for character 21 (number of eye units) that was treated as ordered (command line: ccode +20; [zero-based numbering in TNT]). The tree buffer was set to hold 10,000 trees. The analysis consisted of finding the optimal score 100 times using the default search of xmult- which is running multiple replications, using sectorial searches, drifting, ratchet and fusing combined- and 10 cycles of tree drifting (command line: hold 10000; sec:slack 15; xmu = hit 100 drift 10;). A strict consensus (Nelsen tree; command line: nelsen*;) was obtained, on which jackknife support values (Farris et al., 1996) with 36% resampling, 1000 replications (command line: resample = jak replic 1000 probability 36) and Bremer support (Bremer, 1988; 1994) were calculated. Unambiguous characters were mapped using WinClada (Nixon, 2002), where branches without supporting characters were collapsed.

SYSTEMATIC PALEONTOLOGY

Order Hemiptera Latreille, 1810

Suborder Sternorrhyncha Amyot and Audinet-Serville, 1843

Superfamily Coccoidea Fallén, 1814

Family Weitschatidae Koteja, 2008

Type Genus: *Weitschatus* Koteja, 2008.

Family Diagnosis (macropterous male): Weitschatidae differs from other families by the combination of the following characters: antennal capitate setae absent (vs. present in Arnoldidae), pterostigma present on the forewing (vs. absent in Xylococcidae, Arnoldidae, Grohnidae, Serafinidae, and *Xiphos,* n. gen.), undifferentiated tarsal digitules (vs. clavate in Arnoldidae and *Xiphos,* n. gen.), small caudal extensions present or absent.

Genera Included: *Weitschatus* Koteja and *Pseudoweitschatus,* n. gen.

Comments: *Pseudoweitchatus* is a xylococcid-like genus, classified here in the family Weitschatidae based on the presence of a pterostigma on the forewing, a structure that is otherwise known only in *Weitschatus* among the xylococcid-like genera. This feature is found in Recent Margarodidae, but also Jersicoccidae (although only ventrally, Koteja [2000b]), Grimaldiellidae, Lebanococcidae, and *Xiphos,* n. gen. (see description below). *Weitschatus* differs from *Pseudo-*

weitschatus by the latter having a bilobed hamulohaltere and a small caudal extension on tergite VIII (Koteja, 2008). Therefore, by adding *Pseudoweitschatus* in the family Weitschatidae we here updated the family diagnosis to include variation between *Pseudoweitschatus* and *Weitschatus.*

Our phylogenetic results (see below) retrieved *Pseudoweitschatus* as sister group to *Weistchatus* and the family as sister group to Xylococcidae.

Pseudoweitschatus, new genus

Type Species: *Pseudoweitschatus audebertis,* n. sp., by present designation and monotypy.

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

Etymology: The generic name refers to the close similarity of this genus to *Weitschatus* Koteja described in Koteja (2008). Gender: masculine.

Generic Diagnosis (macropterous male): *Pseudoweitschatus,* n. gen., differs from *Weitschatus* by the combination of the following characters: antennal apical segment with curved bristles (vs. absent); hamulohaltere leaf-shaped (vs. bilobed); claw digitule spinose (vs. clavate); dorsal abdominal segments VII and VIII each with a single row of tubular ducts (vs. two to four rows of pores); small caudal extensions absent (vs. present); penial sheath triangular and short.

Included Species: *P. audebertis,* n. sp.

Pseudoweitschatus audebertis, new species

Figures 1A, 2

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

Type: Holotype AMNH Bu-1416 alate male, in a 10 × 8 × 2 mm rectangular, bright orange, transparent polished amber piece; specimen in good condition, but thoracic structures significantly shriveled, 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 the American Museum of Natural History.

Etymology: The epithet is in reference to Vincent Audebert, the first author's high school biology 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 creates 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 compound eyes (fig. 2A). Dorsal midcranial ridge well developed and extending to a strongly sclerotized postoccipital ridge (fig. 2A), setae present 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 (fig. 2B). **Antenna** (fig. 2C): 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

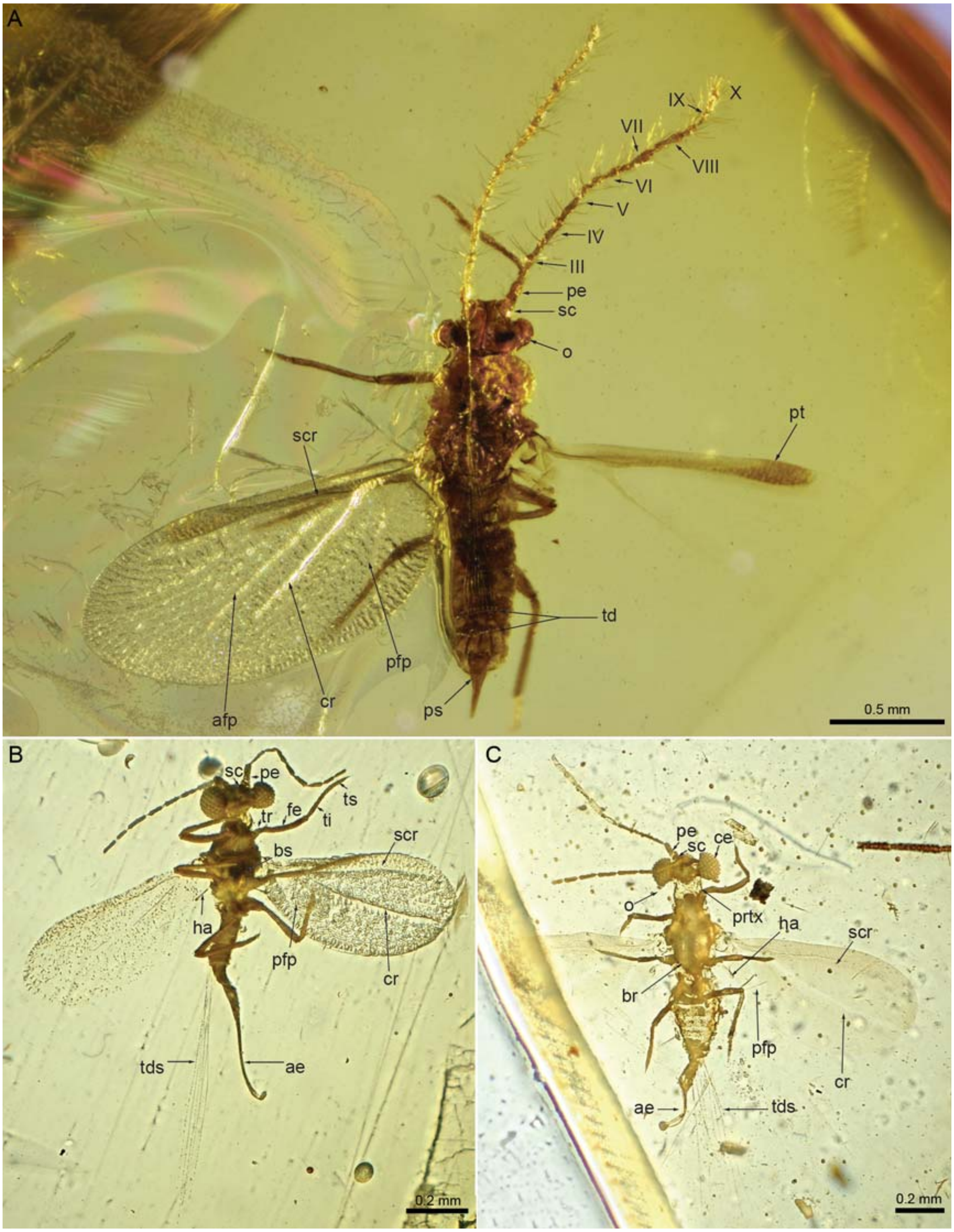


FIGURE 1. Photomicrographs of (**A**) Dorsal view of *Pseudoweitschatus audebertis,* n. sp., holotype AMNH Bu-1416. (**B**) Ventral view of *Kozarius perpetuus,* n. sp., holotype AMNH Bu-1163. (**C**) Ventral view of *K. achronus,* n. sp., holotype AMNH Bu-233a.

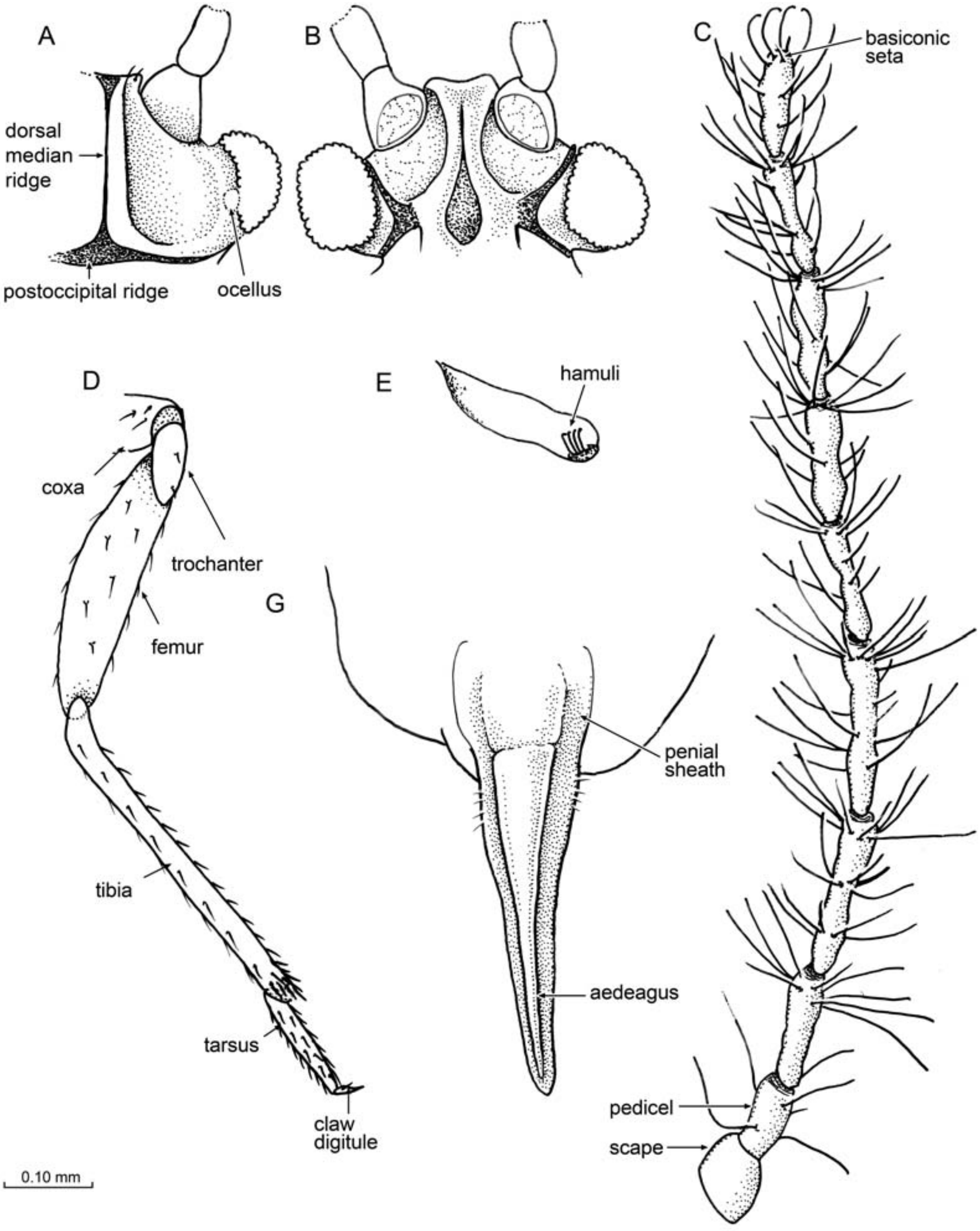


FIGURE 2. Details of *Pseudoweitschatus audebertis,* n. sp. (**A**) Dorsal view of head. (**B**) Ventral view of head. (**C**) Antenna. (**D**) Leg. (**E**) Hamulohaltere. (**G**) Ventral view of penial sheath.

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 (unclear whether this is due to shriveling of the thoracic structures), scutellum with strongly sclerotized ridges. Ventral thoracic structures obscured. **Wings** (fig. 1A): 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 3/4 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 (fig. 2E) large and elongate, leaf shaped, ca. 210 µm long, 50 µm wide; each with four hamuli attached on anterodistal margin. **Legs** (fig. 2D): 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 hairlike setae; tibia: 342 long µm, 22 µm wide, with short spinelike setae, tibial spurs not differentiated; tarsus 2-segmented (second segment short and triangular), 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 small 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** (fig. 2G): Penial sheath originating posteroventrally to anus, triangular, 275 µm long, 80 µm wide at base, narrowing from about 1/2 length of penial sheath, with short setae present anteriorly. Aedeagus slender and pointed at the apex. Eversible endophallus probably present inside.

Kozariidae, new family

Type Genus: *Kozarius*, n. gen., by present designation and monotypy.

Diagnosis: Kozariidae differs from other fossil families by the combination of the following characters: body minute, head large, compound eyes bulging, with less than 100 ommatidia; antenna with filiform segments, capitate and fleshy setae on apical segment; prescutum vertically elongate (vs. oval or horizontally elongate in other families), without prescutal setae, scutellum rhombus or subrhombus shaped; wings hyaline, without microtrichia or pterostigma, with a subcostal ridge extending to 3/4 wing length, cubital ridge and posterior flexing patch present; hamulohalteres present, long and narrow (leaf shaped in several archaeococcoid families, but similar to, e.g., Ortheziidae); legs slender, tarsus 1-segmented, shorter than tibia; claw thin and elongate, almost uncurved, claw digitules slightly clavate, claw denticle absent; abdomen with tubular ducts on tergites VI and VII. Genital segment with exceptionally elongate and apically curved penial sheath.

Genus Included: *Kozarius,* n. gen.

Comments: Kozariidae is unique among families based on the shape of the prescutum, particularly in its being elongate vertically. Most of the other families have an oval to round prescutum, and if elongate it is always horizontal (e.g., Xylococcidae). *Kozarius* shows some similarities with *Matsucoccus* Cockerell, 1909. The head structure overall resembles that of *Matsucoccus*, especially the general shape, the apical flagellar segment bearing capitate setae and curved bristles, and the protruding compound eyes. The short mesopostnotum is also reminiscent of *Matsucoccus*. However, there are other obvious features that differ significantly from *Matsucoccus*: the presence of tubular ducts on segments VI and VII (vs. only present on segment VII 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). Additionally, Matsucoccidae is one of the most morphologically 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 ornamentation 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 strongly conserved, showing little variation among Recent and fossil Matsucoccidae. *Kozarius* does not bear pennate ridges on the forewings (very reduced venation). Therefore, it can be excluded from the Matsucoccidae. Moreover, our phylogenetic analysis retrieved the family as monophyletic and was included in an extinct lineage comprised of Lebanococcidae, *Alacrena,* n. gen., and *Xiphos,* n. gen., both considered incertae sedis, as well as Burmacoccidae in Burmese amber. Despite the rough similarity to Matsucoccidae, *Kozarius* does not seem to be related to this family.

Kozarius, new genus

Type Species: *Kozarius perpetuus,* n. sp., designated here.

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

Etymology: Patronym in tribute to the late Ferenc Kozár (1943–2013), who contributed greatly to the study of scale insects during his distinguished career. Gender: masculine.

Diagnosis: As for family.

Species Included: *K. perpetuus,* n. sp., and *K. achronus,* n. sp.

Kozarius perpetuus, new species

Figures 1B, 3

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

Type: Holotype AMNH Bu-1163, alate male, in a 5 × 3 × 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 wax projections 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 "continual, continuing without interruption".

Diagnosis: *Kozarius 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 completely developed and strong (vs. developed only on posterior half of basisternum); penial sheath longer and thinner, 1/3 body length (vs. 1/5).

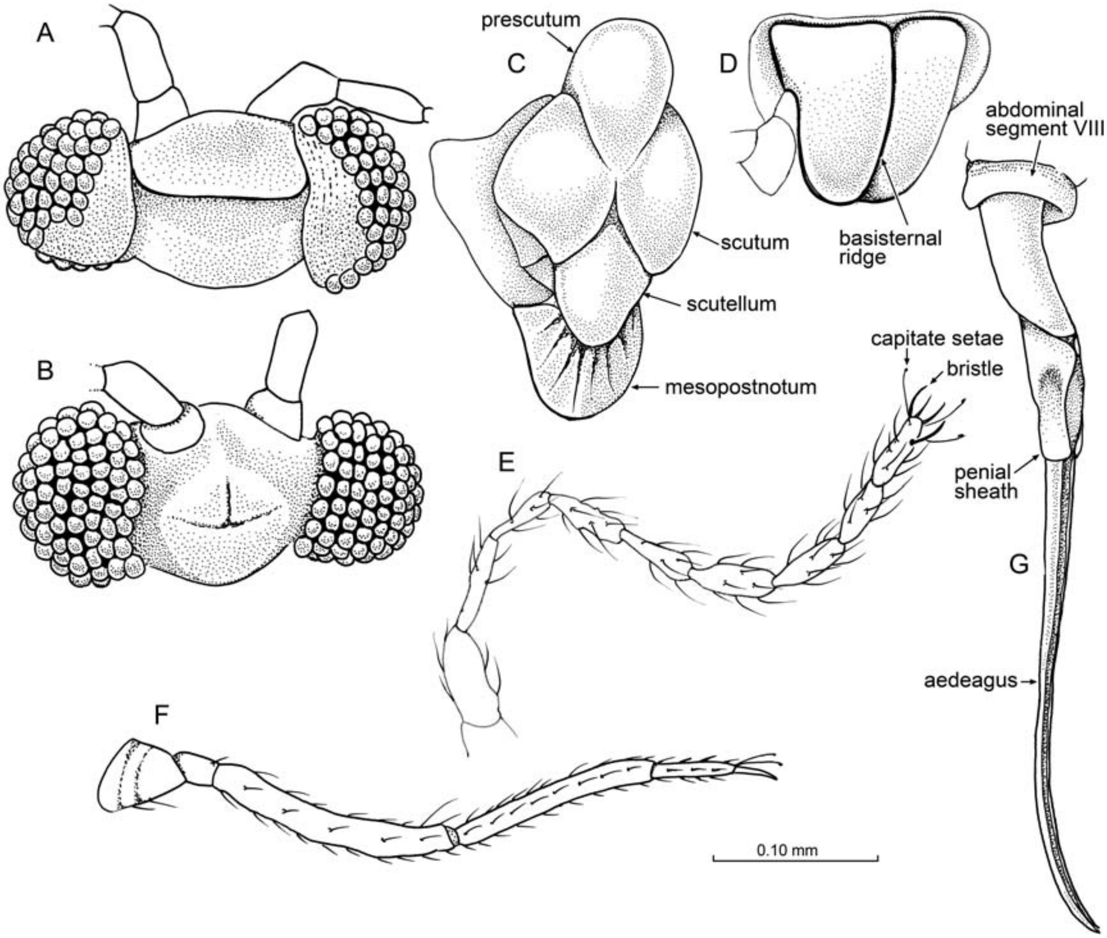


FIGURE 3. Details of *Kozarius perpetuus,* n. sp. (**A**) Dorsal head. (**B**) Ventral view of head. (**C**) Dorsal view of mesothorax. (**D**) Basisternum. (**E**) Antenna. (**F**) Leg. (**G**) Side view of penial sheath.

Description: Body relatively small, total length 1.02 mm, greatest width at mesothorax, 200 µm. **Head** (fig. 3AB): 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** (fig. 3E): 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 hairlike setae of same length as setae of other flagellar segments. **Thorax:** Head and thorax separated by a strongly constricted neck (fig. 1B). 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; mesopostnotum almost as long as scutellum (fig. 3C). *Ventrally*: basisternum 112 µm long, 120 µm wide, with a strong median ridge, with setae dicernable, anterior part of basisternum shorter than posterior part (fig. 3D). **Wings** (fig. 1B): 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 3/4 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** (fig. 3F): 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 hairlike setae; tibia 148 µm long, 15 µm wide, with hairlike setae becoming spurlike ventrally; tarsus 1-segmented, 60 µm long,13 µm wide, tibial spurs undifferentiated but tarsal digitule present; claw thin, 25 µm long, almost uncurved, claw digitule and 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 VI and VII 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** (fig. 3G): Penial sheath extremely elongate (455 µm long), 1/3 the body length, 35 µm wide. Aedeagus slender, pointed at apex as long as penial sheath. Eversible endophallus absent.

Kozarius achronus, new species

Figures 1C, 4

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

Type: Holotype AMNH Bu-233a, alate male at the edge of a 10 × 10 × 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, 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"), with the alpha-privative, to mean "timeless, intemporal", referring to the specimen being frozen in time in the amber.

Diagnosis: See *Kozarius perpetuus,* n. sp.

Description: Body relatively small, total length 1.13 mm long, largest width at mesothorax, 260 µm. **Head** (fig. 4AB): 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 (fig. 4A), posterior to compound eyes. Dorsal midcranial ridge present (fig. 4B), 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 (fig. 4A). **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 (fig. 4E), 2 curved bristles and ca. 10 hairlike 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

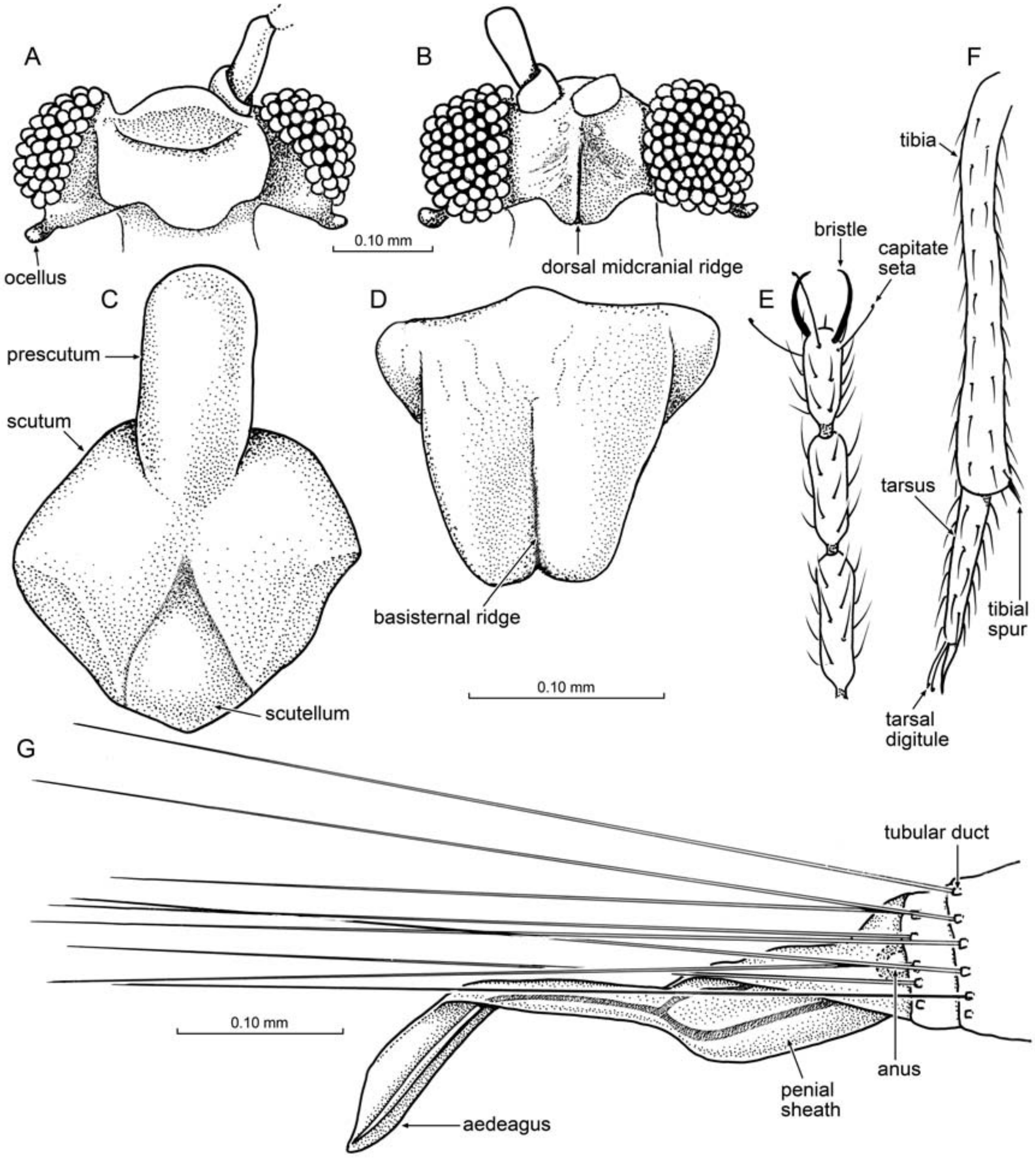


FIGURE 4. Details of *Kozarius achronus,* n. sp. (**A**) Ventral view of head. (**B**) Dorsal view of head. (**C**) Dorsal view of mesothorax. (**D**) Basisternum. (**E**) Apical antennal segments. (**F**) Leg from tibia. (**G**) Dorsal view of posterior abdominal segments and penial sheath, with wax filaments.

dorsally (fig. 4C): prescutum very elongate, bulging anteriorly, without setae; scutum without membranous area, scutellum of subrhombus shape. *Ventrally* (fig. 4D): basisternum 160 μm long, 160 μm wide, with a median ridge only present posteriorly. Anterior part of basisternum shorter than posterior part. **Wings** (fig. 1C): Forewings oval with an intermediate width at base, apex rounded; 845 μm long, 90 μm widest; 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

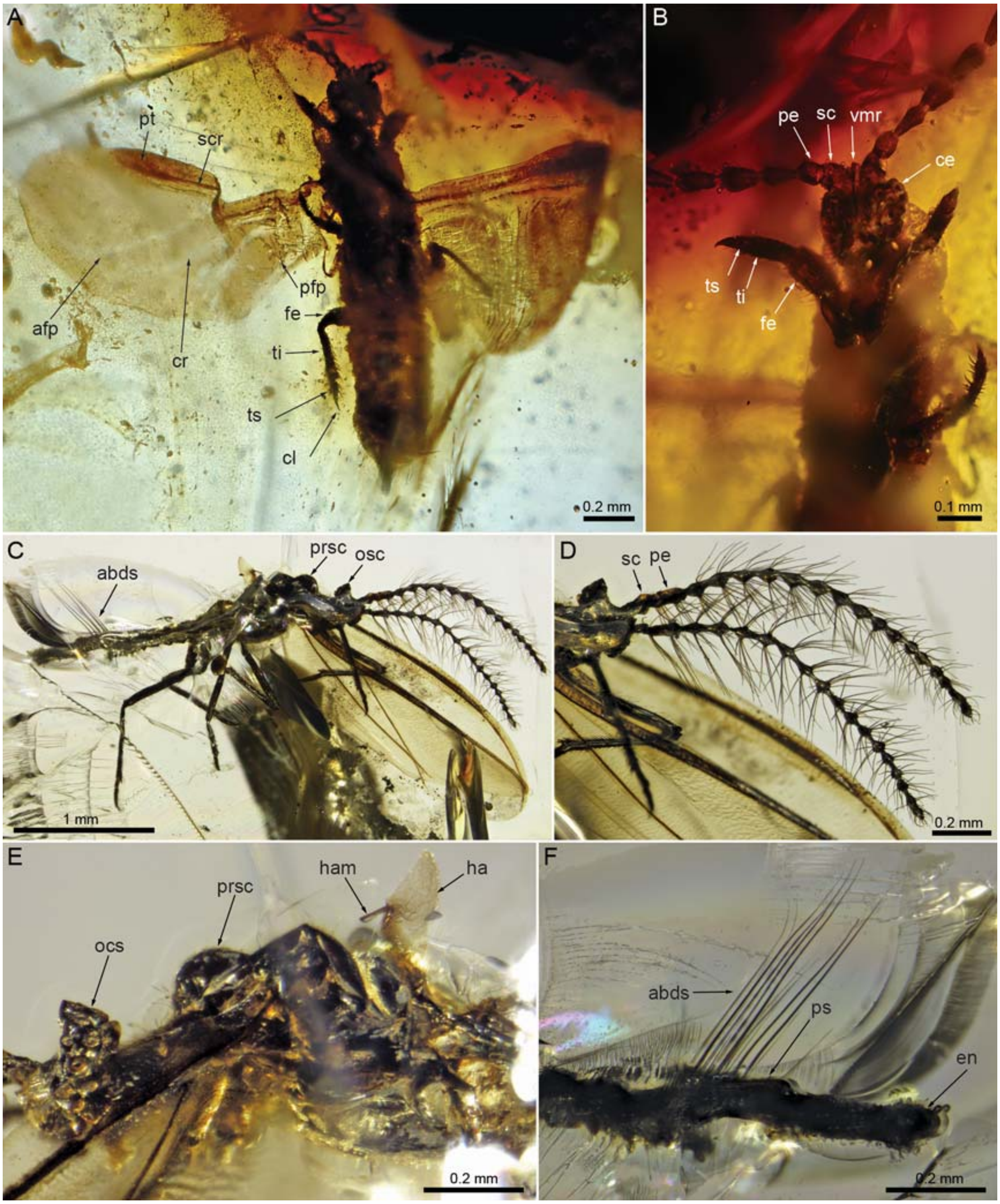


FIGURE 5. Photomicrographs of *Heteromargarodes hukamsinghi,* n. sp., holotype Tad-139. (**A, B**). (**A**) Full ventral view. (**B**) Enlarged ventral view of head and thorax. *Hodgsonicoccus patefactus,* n. sp., holotype AMNH LAE-93 (**C–F**). (**C**) Lateral side. (**D**) Antennae. (**E**) Head and thorax from lateral side. (**F**) Lateral side of penial sheath.

microtrichia absent. Alar fold present. Hamulohalteres present, long and narrow, 90 μm long, with two hamuli. **Legs:** Long and slender, cuticular reticulations absent. Prolegs: coxa triangular, 55 μm long; trochanter and femur about 27 μm wide, together 200 μm long, with hairlike setae, tibia 105 µm long, 16 µm wide, with hairlike setae becoming spinelike ventrally, tibial spurs undifferentiated; tarsus 1-segmented (fig. 4F), 40 µm long, 14 µm wide, tarsal digitules present and finely clavate; claw thin, 20 µm long, claw digitules or denticles not observed. **Abdomen:** Broad (370 µm long without genital segment; 200 µm 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 VI and VII, each with a row of ca. 10 tubular ducts. **Genital segment:** Penial sheath extremely elongate (about 255 µm long), about 1/5 body length, 60 µm widest, proximally and distally enlarged and medially narrow; aedeagus slender and pointed at apex. Eversible endophallus absent.

Family Margarodidae Cockerell, 1899

Heteromargarodes Jakubski, 1965

Type Species: *Heteromargarodes americanus* Jakubski, 1965; by original designation and monotypy.

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

Generic Diagnosis (macropterous male): *Heteromargarodes* differs from other genera of the Margarodidae with the following combination on characters: bifurcated setae absent on legs (vs. present), compound eyes with large ommatidia and almost forming sclerites surrounding the head (vs. definite lateral compound eyes), prothoracic legs significantly shorter than mesothoracic legs (vs. not significantly shorter).

Species Included: *Heteromargarodes americanus* Jakubski, 1965, *H. chukar* (La Rivers, 1967), *H. hiemalis* (Cockerell, 1899), *H. hukamsinghi,* n. sp.

Comments: *Heteromargarodes* was defined based on adult female morphology and originally included only *H. americanus* Jakubski, 1965. Unruh and Gullan (2007) later transferred *Margarodes chukar* (La Rivers, 1967) and *Porphyrophora hiemalis* (Cockerell, 1899) to the genus based on "(i) raised bare patches on the derm, (ii) long hairlike body setae, and (iii) sievelike multilocular pores" (Unruh and Gullan, 2007: 171). All species of Recent *Heteromargarodes* are distributed in North America. The adult males of *H. americanus* and *H. ?chukar* have been described (Hodgson and Foldi, 2006). At the time of the description *H.?chukar* was assigned to *Margarodes*, and based on comparison with *Margarodes prieskaensis* (Jakubski, 1965), the authors already doubted the assignment of this species to *Margarodes*, although they did not suggest a potential genus transfer. Additionally, it is possible that the specimen identified and described in Hodgson and Foldi (2006) is not *H. chuckar*, thus the generic diagnosis is here based only on the morphology of *H. americanus* and *H. hukamsinghi,* n. sp.

Heteromargarodes hukamsinghi, n. sp., is assigned within this genus based on the description of the adult male of *Heteromargarodes americanus.* Given the morphological variation among genera in Margarodidae sensu stricto, provided in Hodgson and Foldi (2006), namely *Dimargarodes* Silvestri, 1938, *Heteromargarodes*, *Margarodes* Guilding, 1829, *Neomargarodes* Green, 1914, and *Porphyrophora* Brandt in Brandt and Ratzeburg, 1833, *Heteromargarodes* is the probable genus to which *H. hukamsinghi,* n. sp., belongs, as based on the following features: general shape of antennal segments, each more enlarged proximally (this feature is found in *H. americanus* although in *H.*

chuckar the antennal segments are significantly shortened); the shape of compound eye, almost forming a plate surrounding the head (most resembling *H. americanus*); the legs slender in appearance, with fossorial prolegs significantly shorter than the meso- and metathoracic legs (as opposed to other genera of the family); and by the absence of bifurcated setae on the legs. The phylogenetic analysis retrieved *H. hukamsinghi,* n. sp., within the family Margarodidae, related to *Heteromargarodes americanus* and *Porphyrophora hameli* Brandt, 1833, although there is no further resolution. In general, too few Margarodidae males are currently known and future interspecific variation assessments could provide a more definitive assignment of this fossil species. This fossil constitutes the first occurrence of the family Margarodidae sensu stricto in the fossil record.

Heteromargarodes hukamsinghi**,** new species

Figures 5A–B, 6

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

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

Etymology: Patronym for Hukam Singh of the 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 *H. americanus* described in Hodgson and Foldi (2006) based on the following characters: leg setae spinose (vs. hairlike), large bristles on flagellar segments absent (vs. present), penial sheath longer.

Description: Body large, robust, parallel sided, total length 1.6 mm, 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. 30–40 large ommatidia. Ocelli not visible, but probably present. Dorsal ridges, if present, not observable. Ventrally with a well-developed midcranial ridge (fig. 6A), extending to and meeting compound eyes. Antenna at least 9-segmented (apical segments lost on holotype, fig. 6B); lengths of segments (in µm): scape 70–75, with less than 10 strong setose setae; pedicel 60–68, with numerous hairlike 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 hairlike 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 visible dorsally or ventrally due to debris and darkness of amber). **Wings** (fig. 5A): 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 3/4 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 reticu-

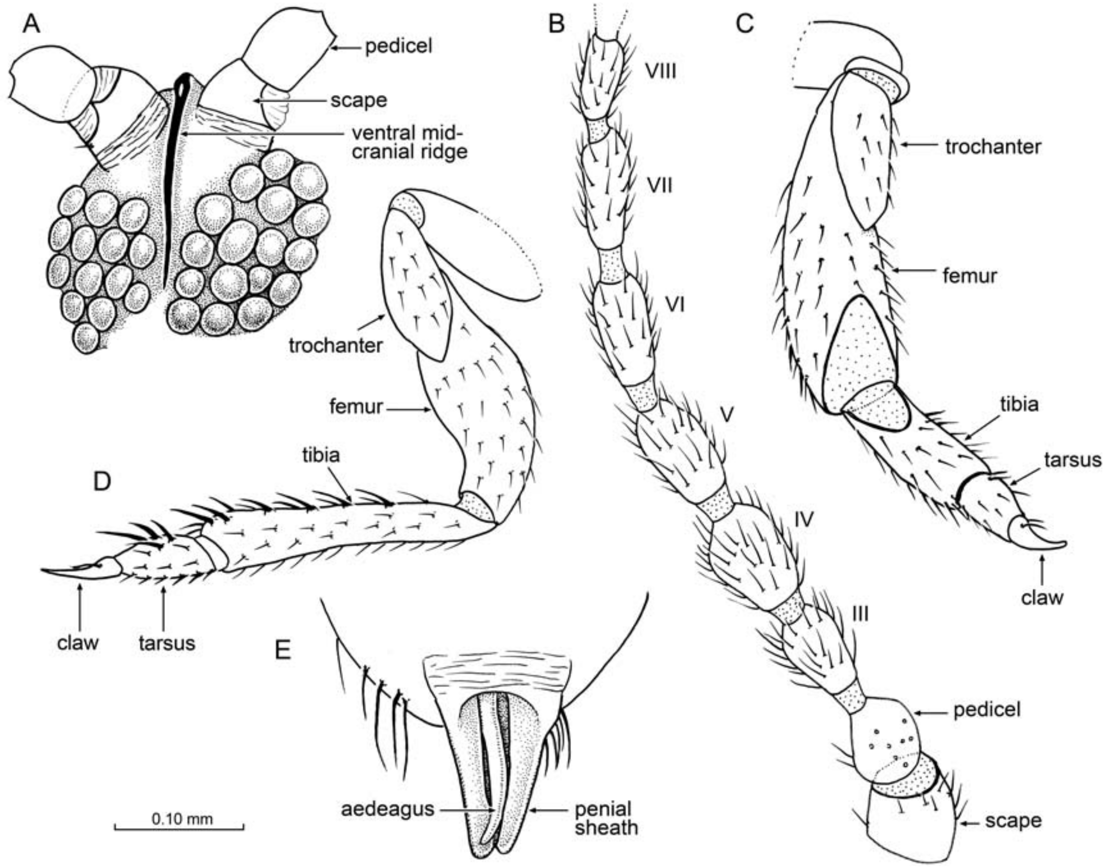


FIGURE 6. Details of *Heteromargarodes hukamsinghi,* n. sp. (**A**) Ventral view of head. (**B**) Antenna, (**C**) Fore leg. (**D**) Hind leg. (**E**) Ventral side of penial sheath.

lations absent, prolegs fossorial. Prothoracic legs (fig. 6C): coxa not visible; combined length of trochanter + femur 215 µm, 88 µm wide, with hairlike setae, bifurcated setae absent. Tibia 90 µm long, 45 µm wide, with hairlike setae becoming spinelike ventrally (tibial spurs), bifurcated setae absent; tarsus 1-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 (fig. 6D): coxa elongate, 130 µm; trochanter + femur 245 µm, 73 µm widest, with numerous hairlike setae, bifurcated setae absent; tibia 210 µm, with numerous spinelike setae and tibial spurs on ventral margin, bifurcated setae absent; tarsus 82 µm, with spinelike setae, with a longer ventral seta 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** (fig. 6E): 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.

Hodgsonicoccidae, new family

Type Genus: *Hodgsonicoccus,* n. gen., by monotypy and present designation.

Diagnosis: Hodgsonicoccidae differs from other families by the combination of the following characters: body exceptionally large (ca. 2 mm), head with two ocular sclerites, each bearing less than 20 large and protruding simple eyes (vs. compound eyes, rows of simple eyes or two pairs of eyes in all other Coccoidea); antenna long, with binodose flagellar segments, each with long setae organized in whorls (similar to Monophlebidae), each becoming shorter distally; forewings elongate and narrowed apically, subcostal ridge extending to tip of wing, cubital ridge present, membrane with microtrichia (vs. absent in other archaeococcoids with compound eyes); hamulohaltere large and broad, with microtrichia (vs. absent in all Coccoidea), three hamuli inserted on anterior margin (vs. at the tip of hamolohaltere for all other Coccoidea); abdomen with several long, spinose setae on posterior segments; penial sheath triangular, with a large, everted endophallus.

Genus Included: *Hodgsonicoccus,* n. gen.

Comments: Several features found in Hodgsonicoccidae make this new fossil family quite remarkable: (1) the eye structure was here interpreted as two ocular sclerites because they completely surround the head, as opposed to laterally located compound eyes. These sclerites, however, bear multiple rows of large simple eye facets. So far, all Recent families of coccoids bear either compound eyes or ocular sclerites with either a single row of multiple or two pairs of simple eye facets. According to the research by Koteja and Azar (2008), however, *Palaeotupo danieleae* Koteja and Azar, 2008, seems to present ocular sclerites with two rows of multiple simple eye facets. This type of eye structure could possibly indicate an intermediate state between compound eyes with multiple ommatidia and one with reduction of the eyelets to two pairs, as in neococcoid families. (2) The binodose antennal segments with whorls of setae, however, are similar to archaeococcoids, such as are found in some Recent Monophlebidae genera (e.g., *Drosicha*) as well as in extinct Jersicoccidae (Koteja, 2000b). (3) Both forewing and hamulohaltere are also peculiar: the generally elongated shape of the forewing is similar to Jersicoccidae and venation (subcostal ridge extending to tip of wing) is similar to, for instance, Recent Putoidae and extinct Labiococcidae. The hamulohaltere, although enlarged for a coccoid, is significantly reduced as compared with aphid hind wings. The position of the hamuli is particularly anteriad and is similar to that of hooked hamuli on developed hind wings of aphids, possibly suggesting a plesiomorphic state to Coccoidea. The presence of microtrichia on hamulohalteres is intriguing as in Coccoidea, when present, microtrichia are generally on the forewings (absent in archaeococcoids with compound eyes) (Hodgson and Foldi, 2006). (4) Bifurcated setae are present in some Margarodidae, Stigmacoccidae, and Kuwaniidae, and all Monophlebidae and Coelostomidiidae (Hodgson and Foldi, 2006), although none of these recent families present the same combinations of characters as found in Hodgsonicoccidae. (5) Finally, the last abdominal segments present long and extremely sclerotized setae projecting posteriorly, unique to this family. Overall, the combination of the striking features listed above is unknown among Coccoidea and therefore justifies the creation of a new family.

Probably the most similar taxon to Hodgsonicoccidae is extinct Jersicoccidae, represented by *Jersicoccus*, described from New Jersey amber (Koteja, 2000b). *Jersicoccus* has a similar elongated forewing shape and binodose antennal segments, but the eyes are definitely compound, with numerous ommatidia, and waxy filaments are present on the abdomen, suggesting the presence of tubular ducts, absent in *Hodgsonicoccus*. Furthermore, our phylogenetic results retrieved *Hodgsonicoccus* as sister group to other taxa without compound eyes, whereas Jersicoccidae was retrieved as sister family to all Coccoidea.

Hodgsonicoccus, new genus

Type Species: *Hodgsonicoccus patefactus,* n. sp., by present designation and monotypy.

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

Etymology: The genus is named after 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 family.

Species Included: *H. patefactus,* n. sp.

Hodgsonicoccus patefactus, new species

Figures 5C–F, 7

Type Locality: Lebanon: North Lebanon: Bchare Mountain. Early Cretaceous.

Type: Holotype AMNH LAE-93, alate male in a 8 × 2.5 × 2 mm 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: second or third instar nymph of undescribed Coccoidea.

Etymology: The epithet is from the Latin participle of *patefactus*, meaning "discovered, revealed".

Diagnosis: As for genus.

Description: Body large, total length 2.04 mm, largest width at mesothorax, ca. 500 µm. **Head** (fig. 5E): Short, 290 µm wide, 185 µm long, with well-developed ocular sclerites surrounding most of head, bearing 10–15 large, simple eyes (fig. 7A). Ocelli present dorsally. Head ridges not observable. **Antenna** (fig. 5D, 7B): 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 toward apical segment (300 µm for setae on proximal segments to 90 µm for apical segment). Apical segment also bearing basiconal setae and curved bristles. **Thorax** (fig. 5E): 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. *Ventrally*: prothoracic structure not visible; basisternum large, with a median ridge, setae not observed. **Wings** (fig. 7D): 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 (fig. 7E) large

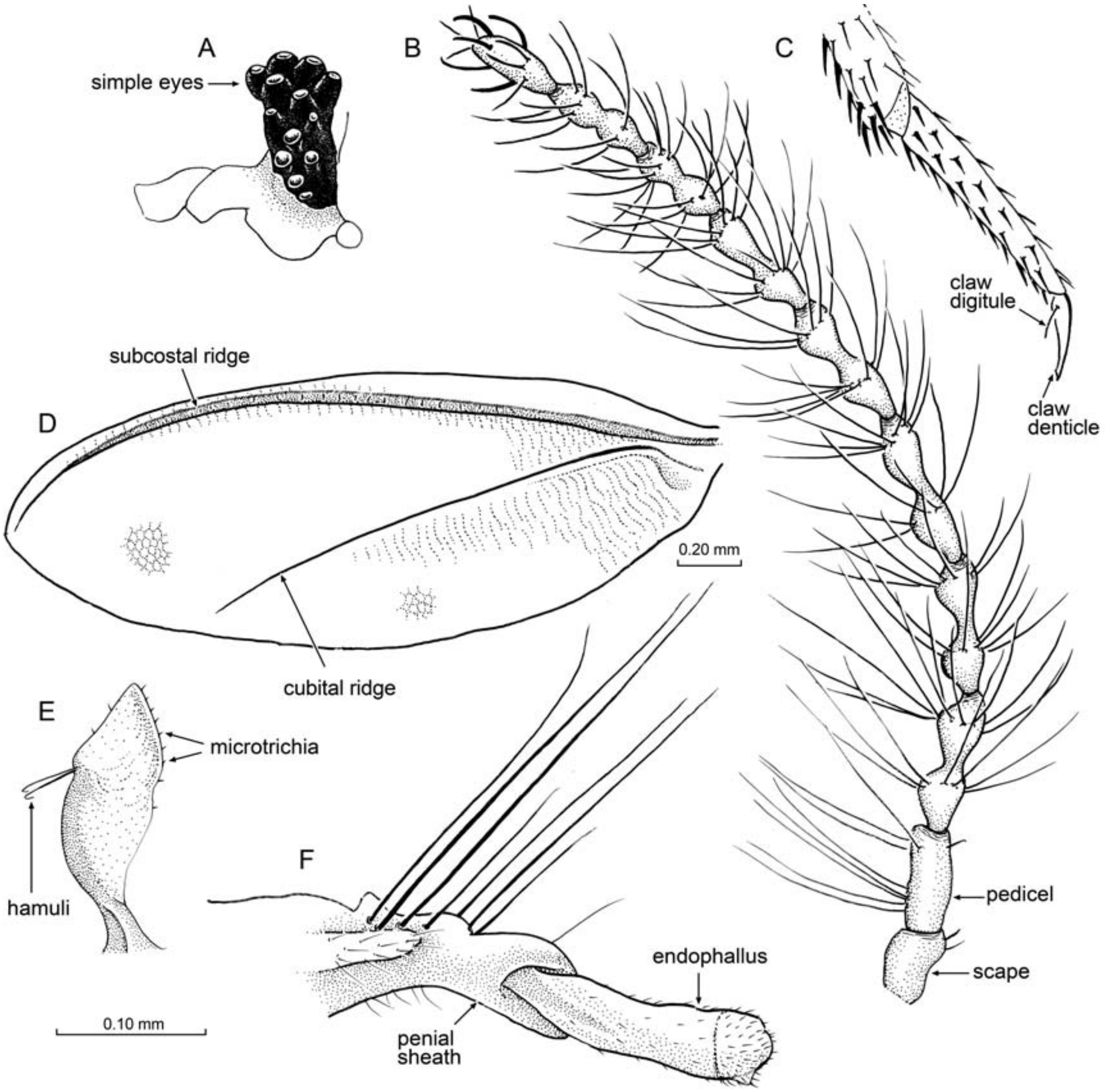


FIGURE 7. Details of *Hodgsonicoccus patefactus,* n. sp. (**A**) Head from right lateral view. (**B**) Antenna. (**C**) Tarsus and claw. (**D**) Fore wing. (**E**) Hamulohaltere. (**F**) Left lateral view of penial sheath.

and leaf shaped, ca. 290 µm long, 85 µm wide; with microtrichia, with 3 hamuli located on anterior margin of hamulohaltere. **Legs** (fig. 7C): 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 hairlike setae, with a few bifurcated setae; tibia: 470 µm long, 30 µm wide, with strong hairlike setae becoming spinelike ventrally and bifurcate; tarsus 2-segmented, 180 µm long, 30 µm wide, tarsal spurs and digitules undifferentiated; claw thin, 40 µm long, virtually uncurved, with spinose claw digitules, and a small denticle. **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, spinelike setae (300–

500 µm long) (fig. 7F). Caudal extension absent. **Genital segment** (fig. 7F): Penial sheath triangular. Aedeagus slender and pointed at apex; eversible endophallus present.

Family Pityococcidae McKenzie, 1942

Pityococcus McKenzie, 1942

Type Species: *Pityococcus ferrisi* McKenzie, 1942; by original designation.

Generic Diagnosis (macropterous male): Based on the description of *Pityococcus* sp. in Hodgson and Foldi (2006) and the present description, *Pityococcus* differs from the fossil *Cancerococcus apterus* Koteja, 1988c (*Desmococcus* male is unknown) with the following combination of characters: ocular sclerite with five pairs of simple eyes (vs. four in *Cancerococcus*), wings present (vs. absent in *Cancerococcus*).

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

Species Included: *Pityococcus* was defined based on adult female morphology and includes the Recent *P. deleoni* McKenzie, 1942, *P. ferrisi* McKenzie, 1942, and *P. rugulosus* McKenzie, 1942. Only an unidentified *Pityococcus* was described based on a macropterous male in Hodgson and Foldi (2006).

Comments: Adult males of *Pityococcus* have been frequently found as inclusions in Eocene ambers and, according to Koteja (2000a), all are apterous. Therefore, this is the first formal description of a winged *Pityococcus* male 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*, but most appendages were missing. *Pityococcus moniliformalis,* n. sp., was assigned in this genus based on the following combination of characters: ocular sclerite with 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 our cladogram, *P. moniliformalis* is retrieved as the sister taxon to the Recent *Pityococcus* sp. and Pityococcidae is included in an extinct lineage including *Turonicoccus*, *Pedicellicoccus,* n. gen., *Grimaldiella*, and *Electrococcus*. Koteja discussed the affinity of *Turonicoccus* and *Pityococcus*, with regard to the presence of an everted endophallus (Koteja, 2000b: 176), found for the most part in archaeococcoids with compound eyes (Hodgson and Foldi, 2006). However, Koteja did not have a detailed description of Recent *Pityococcus* at the time, having found only apterous *Pityococcus* in Baltic amber, and relying on the reports of Miller and Miller (1993) and Miller and Gimpel (1999) for Recent representatives of the genus. Given current knowledge, *Pityococcus* is mostly closely related to *Turonicoccus* based on the presence of the endophallus, antennal segments with short and stout fleshy setae, capitate setae on the apical antennal segment (but *Turonicoccus* also bears capitate setae on other antennal segments), but differs by having only five simple eyes (as opposed to six in *Turonicoccus*).

All Recent *Pityococcus* are distributed in the Nearctic region and feed on pine trees. The presence of *Pityococcus* in Palaearctic Baltic ambers indicates that this genus is a relict taxon that was probably more widely distributed in the past.

Pityococcus moniliformalis, new species

Figure 8

Type Locality: Russia: Palmnicken/Yantaryni mines, on the eastern coast of the Baltic Sea. Eocene.

Type: Holotype AMNH Ba-Ve762, alate male in a 5 × 5 × 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 one folded, white milky layers obstructing some parts, such as the head area; accessible views: ventral and dorsal (fig. 8AB). Baltic amber, Palmnicken mines in Yantaryni, on the eastern coast of the Baltic Sea, Russia. Purchased from Jurgen Velten Baltic amber coll., deposited at the American Museum of Natural History.

Etymology: The epithet *moniliformalis* is composed of the Latin *monile,* meaning "necklace" or "collar" and the adjective *formalis* derived from *forma*, meaning "shape." This refers to the round, beadlike antennal segments.

Diagnosis: *Pityococcus moniliformalis* 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** (fig. 8CD): 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** (fig. 8G): 9-segmented, total length 305–375 µm; lengths of segments (in µm) scape 25; pedicel 50; flagellar segments III to X all round, 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 hairlike 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 hairlike setae of the same length as on other flagellar segments. **Thorax** (fig. 8EF): 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** (fig. 8A): 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 3/4 wing length. Additionally to subcostal ridge, only

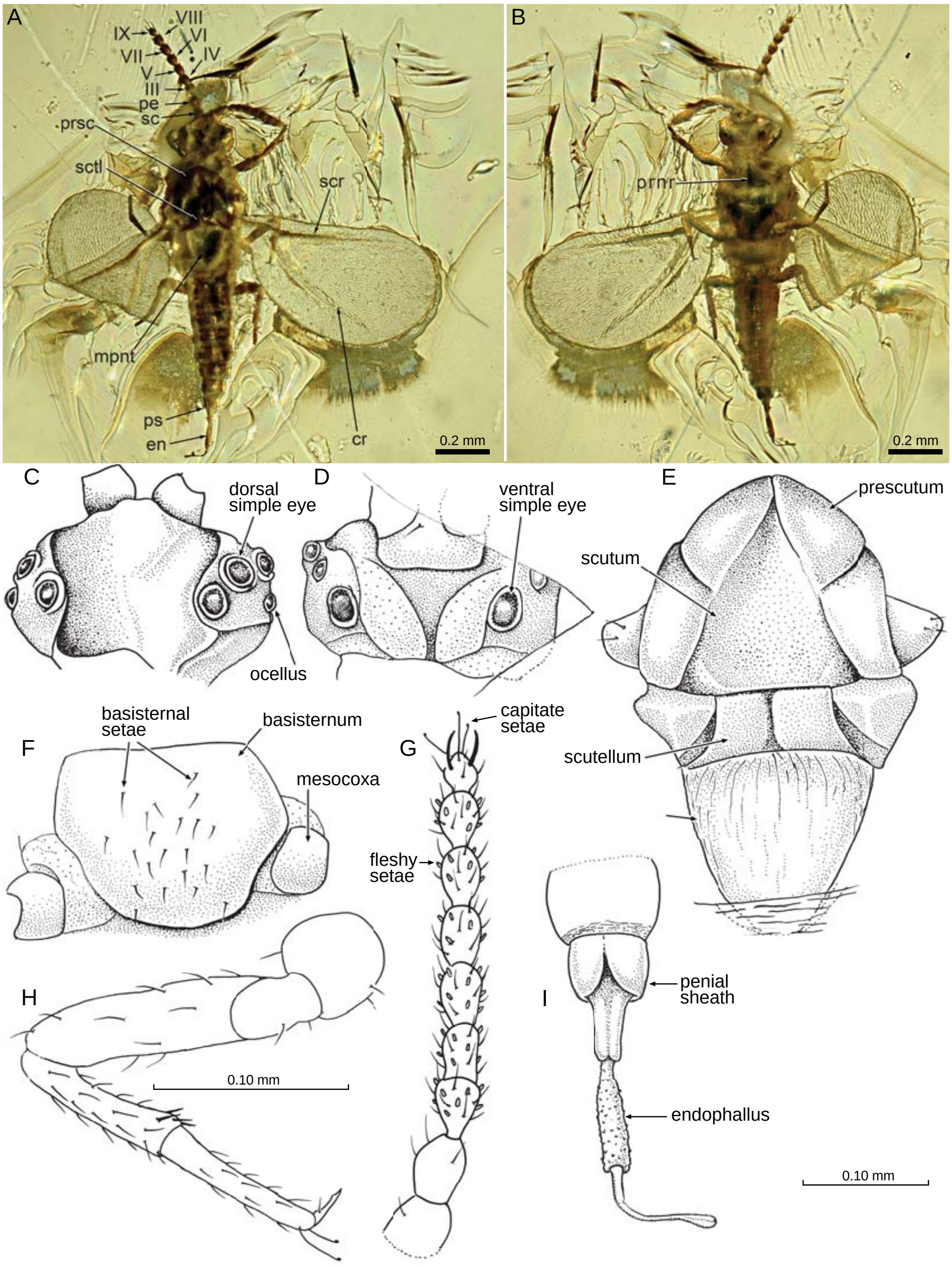


FIGURE 8. *Pityococcus moniliformalis,* n. sp., holotype AMNH Ba-Ve762. Photomicrographs of (**A**) Dorsal and (**B**) ventral surfaces. Details of (**C**) dorsal and (**D**) ventral views of head. (**E**) Dorsal view of mesothorax. (**F**) Basisternum. (**G**) Antenna. (**H**) Leg. (**I**) Ventral view of penial sheath.

cubital ridge present. Alar setae and sensoria not observed, microtrichia present across wing surface Alar lobe present. Hamulohalteres not detected, but probably present. **Legs** (fig. 8H): Subequal in length, cuticular reticulations absent; prolegs: coxa triangular, 50–60 µm long, trochanter and femur fused, 145–155 µm long, with hairlike setae; tibia: 80–90 µm long, with hairlike setae becoming spinelike ventrally; tarsus 2-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** (fig. 8I): penial sheath small (65 µm wide, 105 µm long), almost parallel sided anteriorly for more than 1/3 of length, with few short setae. Aedeagus broader than tip of penial sheath. Endophallus everted, covered with small spines.

Apticoccidae, new family

Type Genus: *Apticoccus* Koteja and Azar, 2008; by present designation.

Family Diagnosis (macropterous male): Apticoccidae differs from *Turonicoccus* and *Electrococcus* by the combination of the following characters: body especially small (less than 800 µm long) (vs. larger); head narrow; antennae 10-segmented, with scape almost meeting anteriorly (vs. not meeting medially); antennal segments shorter distally (vs. of almost equal length), with fleshy setae on flagellar segments and forming a brush on apical segment (vs. not forming a brush); capitate setae absent (vs. present); 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 transversely 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 (vs. narrow in *Turonicoccus*), with two hamuli; penial sheath elongate and pointed, at least 1/7 body length (vs. short and triangular).

Genus Included: *Apticoccus* Koteja and Azar, 2008.

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* Koteja from New Jersey amber and suggested that this genus and *Electrococcus*, described from Canadian amber (Beardsley, 1969), belong to the same family. The assignment of *Apticoccus* to Electrococcidae 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, transverse and narrow (vs. enlarged rectangular scutellum), penial sheath spinelike (vs. shorter triangular penial sheath). The phylogenetic analysis retrieved Apticoccidae as an independent, monophyletic lineage, sister group to all neococcoid families. Furthermore, *Apticoccus* was not found to be related to either *Turonicoccus* or *Electrococcus.*

Apticoccus, Koteja and Azar, 2008

Type Species: *Apticoccus minutus* Koteja and Azar, 2008; by original designation and monotypy.

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: Specimen 628 (Cocc-1720), alate male in a 3 × 2 × 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), and 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 shows two hamuli).

***Apticoccus fortis*, new species**

Figures 9A, 10

Type Locality: Lebanon: Central Lebanon: Mdeyrij/Hammana: Caza Baabda: Mouhafazet Jabal Loubnon. Lower Cretaceous.

Type: Holotype HAM-1669A, alate male, in a 3 × 2.5 × 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 oxidation) and covered by a thin layer of bubbles; accessible views: ventral and dorsal; Dany Azar amber collection, provisionally deposited in the Muséum National d'Histoire Naturelle.

Etymology: The epithet is from the Latin adjective *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 posteriorly, penial sheath round with one pair of short setae, then abruptly thin and curved (ca. 1/5 body length).

FIGURE 9. Photomicrographs of the new species of *Apticoccus*. (**A**) Dorsal surface of *Apticoccus fortis,* n. sp., holotype HAM-1669A. (**B**) Dorsal and (**C**) ventral surfaces of *Apticoccus longitenuis,* n. sp., holotype AD-20.

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** (fig. 10A): 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. **Thorax:** Head and thorax not obviously separated. Prothorax membranous. Ridges on prothorax not definable. *Dorsally*: prescutum suboval, slightly horizontally elongate, well separated from scutum, without prescutal setae. Other mesothoracic structures hidden by wing. *Ventrally*: thoracic structures covered by a layer of bubbles, median ridge on basisternum not detected. **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 3/4 of wing length. Cubital ridge present and originating from base, extending posteriorly to about 1/2 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** (fig. 10B): Long, robust, all subequal in length, cuticular reticulations absent; measurements of second pair of legs provided (forelegs not easily measurable); coxa not entirely visible but probably triangular; trochanter and femur 67 µm long, with few, hairlike setae. Tibia length 100 µm, with few short, hairlike setae; tarsus 1-segmented, 40 µm long, tarsal spurs undifferentiated, tarsal digitules minutely clavate, longer than claw; claw robust, curved, claw digitule and denticle not detected. **Abdomen:** Pear shaped, 323 µm long (200 µm without genital segment), greatest width 117 µm, tapered gradually apicad. Tergites and sternites well developed and segmentation easy to delineate. Abdominal setae, pores and glandular pouches not observable. **Genital segment** (fig. 10C): Penial sheath elongate (123 µm), 1/5 the 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.

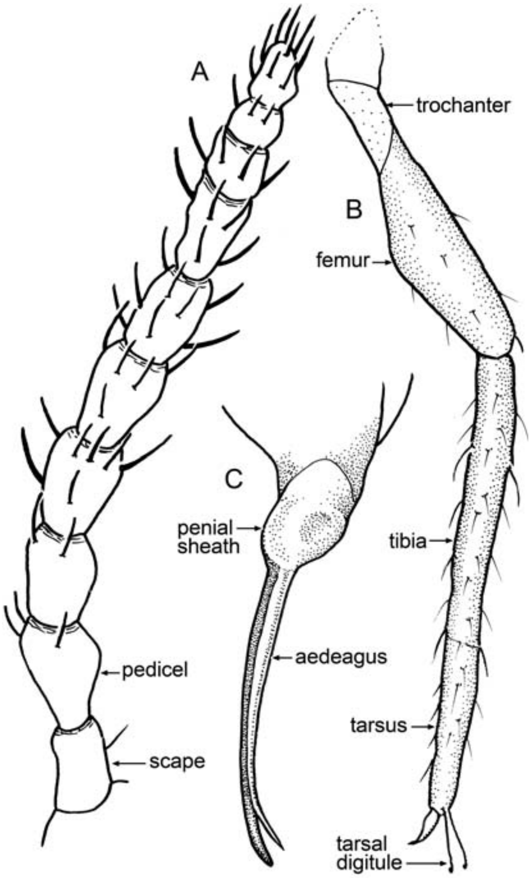


FIGURE 10. Details of *Apticoccus fortis,* n. sp. (**A**) Antenna. (**B**) Leg. (**C**) Ventral view of penial sheath.

Apticoccus longitenuis, new species

Figures 9B–C, 11

TYPE LOCALITY: Lebanon: Central Lebanon: Ain Dara, Caza Baabda, Mouhafazet Jabal Loubnon . Early Cretaceous (Lower Aptian after existing geological maps, but this age is debatable).

TYPE: Holotype AD-20, alate male, in a 3 × 2.5 × 0.5 mm yellow, transparent, rectangular amber piece, embedded in Canada balsam and mounted in epoxy between two coverslips; speci-

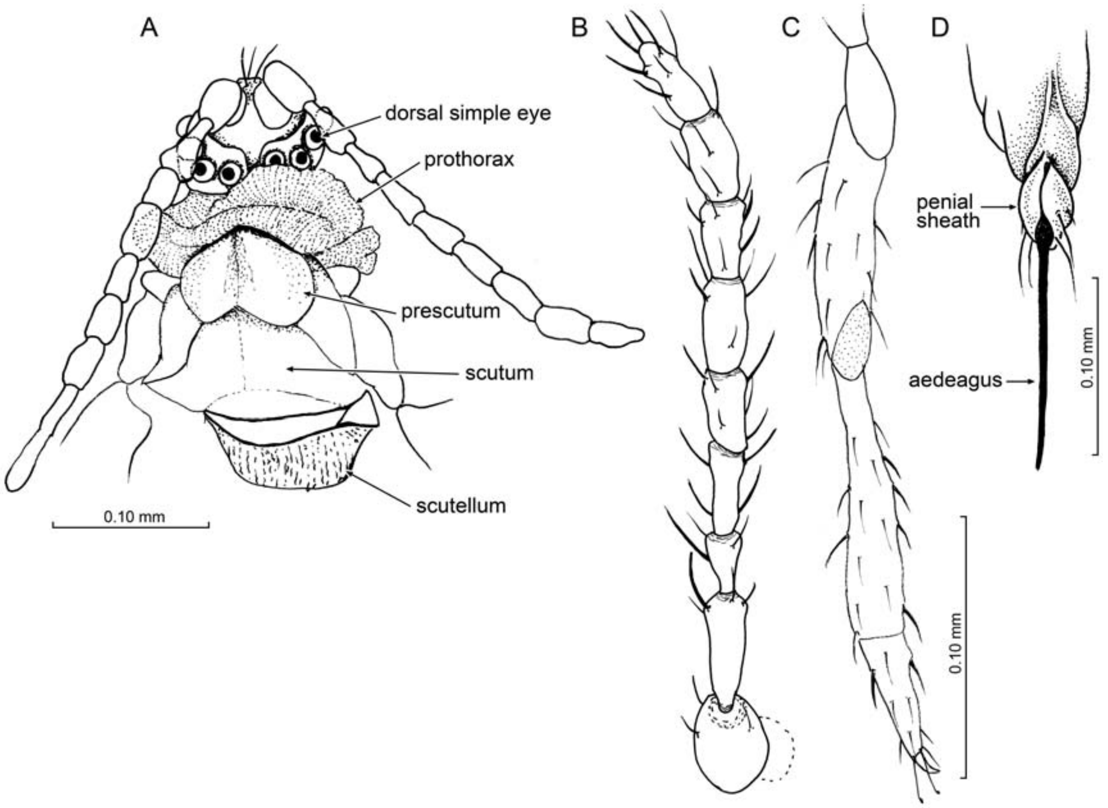


FIGURE 11. Details of *Apticoccus longitenuis,* n. sp. (**A**) Dorsal view of head and thorax. (**B)** Antenna. (**C**) Leg. (**D**) Ventral view of penial sheath.

men 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; Dany Azar amber collection, provisionally deposited in the Muséum National d'Histoire Naturelle.

Etymology: The epithet *longitenuis* comes from the combination of the Latin adjective *longus*, "long," and the Latin adjective *tenuis*, "thin," referring to the long, needle-shaped penial sheath.

Diagnosis: *A. longitenuis* differs from other *Apticoccus* spp. by the following characters: head narrow, thorax wide, abdomen wide but abruptly tapering, penial sheath long and needlelike, ca. 1/4 body length.

Description: Body minute, total length 615 µm, widest at mesothorax, 175 µm. **Head** (fig. 11A): 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** (fig. 11B): 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** (fig.

11A): 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 ventral 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 3/4 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** (fig. 11C): 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 hairlike setae (ca. 10 µm); tibia: 100 µm long, 15 µm wide, with a few hairlike setae, with one differentiated tibial spur; tarsus 1-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** (fig. 11D): 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 needlelike and pointed at apex, not clearly differentiated from penial sheath. Eversible endophallus absent.

Genera incertae familiae

Xiphos, new genus

TYPE SPECIES: *Xiphos vani,* n. sp., by present designation and monotypy.

OCCURRENCE: Lebanon, Central Lebanon (Hammana). Early Cretaceous.

ETYMOLOGY: The generic name *Xiphos* comes from *xiphos*, an ancient Greek double-edged sword, referring to the similar shape of the penial sheath. Gender: masculine.

DIAGNOSIS: Body small but robust, head with two compound eyes bearing 55–60 ommatidia, ocelli found laterally; antennae filiform, weakly trinodose, undifferentiated setae on apical segment; ventral ridges forming a five-armed star, narrow on first 1/2 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 1-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.

SPECIES INCLUDED: *X. vani,* n. sp.

COMMENTS: Assorted features suggest a close relationship with Xylococcidae and related families: the body shape, head with compound eyes, elongate antennae without particular setal differentiation, the wing shape, and the dorsal metathoracic prescutum oval and elongate shaped, triangular scutellum. However, *Xiphos* also possesses a peculiar combination of characters. The presence of a membranous area medially on the scutum is found in Coelostomidiidae and Monophlebidae, and the two lateral areas on the corners of the triangular scutellum is characteristic of the Recent Callipappidae, Coelostomidiidae, and Monophlebidae (but also found in extinct Grohnidae, which was described as a xylococcid-like family). *Xiphos* cannot be assigned to any of these families due to the differences, for instance, in antennal structure (very short setae distributed on one side of the antennal segments in *Callipappus*, and binodose or trinodose segments in Monophlebidae), the very narrow posterior margin of basisternum, and the multiple claw digitules in Coelostomidiidae. Table 2 suggests a close similarity with Grohnidae, although the tarsal digitules in *Xiphos* are clavate. Finally, the elongate and spinelike penial sheath of *Xiphos* is peculiar for any taxa related to Xylococcidae. The other genera with compound eyes and bearing this type of penial sheath are *Kozarius,* n. gen., and *Alacrena,* n. gen. Such an elongate penial sheath is also found in *Burmacoccus* Koteja from Burmese amber, although the compound eyes have significantly less ommatidia. Finally, the morphological phylogenetic analysis indicates that *Xiphos,* n. gen., is sister group to the extinct lineage composed of *Alacrena*, *Lebanococcus,* and *Kozarius,* n. gen. Therefore, *Xiphos* does not seem to be related to xylococcid-like families. For now and until further study, we consider *Xiphos* incertae familiae.

Xiphos vani, new species

Figures 12A–B, 13

Type Locality: Lebanon: Central Lebanon: Mdeyrij/Hammana: Caza Baabda: Mouhafazet Jabal Loubnon. Lower Cretaceous.

Type: Holotype 1215, alate male, in a 6.5 × 5 × 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; Dany Azar amber collection, provisionally deposited in the Muséum National d'Histoire Naturelle.

Etymology: The epithet comes from "Van," in memory of the first author's father, Van Vea (1951–2011).

Diagnosis: As for genus.

Description: Body small but robust, 1.44 mm long total, largest width at mesothorax, 328 µm. **Head** (fig. 13A): 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 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** (fig. 13D): 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, slightly 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 hairlike setae (40–60 µm) and short hairlike setae (25 µm), randomly distributed. Apical segment without bristles or capitate setae. **Thorax** (fig. 13BC): 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

FIGURE 12. Photomicrographs of (**A**) dorsal and (**B**) ventral surfaces of *Xiphos vani,* n. sp., holotype 1215. (**C**) Dorsal surface of *Alacrena peculiaris,* n. sp., holotype AMNH Bu-1516.

μm wide, 70 μm long), with two lateral areas. Mesopostnotum short (45 μm long). **Wings** (fig. 12A): 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 3/4 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** (fig. 13E): Long and robust, cuticular reticulations absent; prolegs: coxa 60 μm long; trochanter and

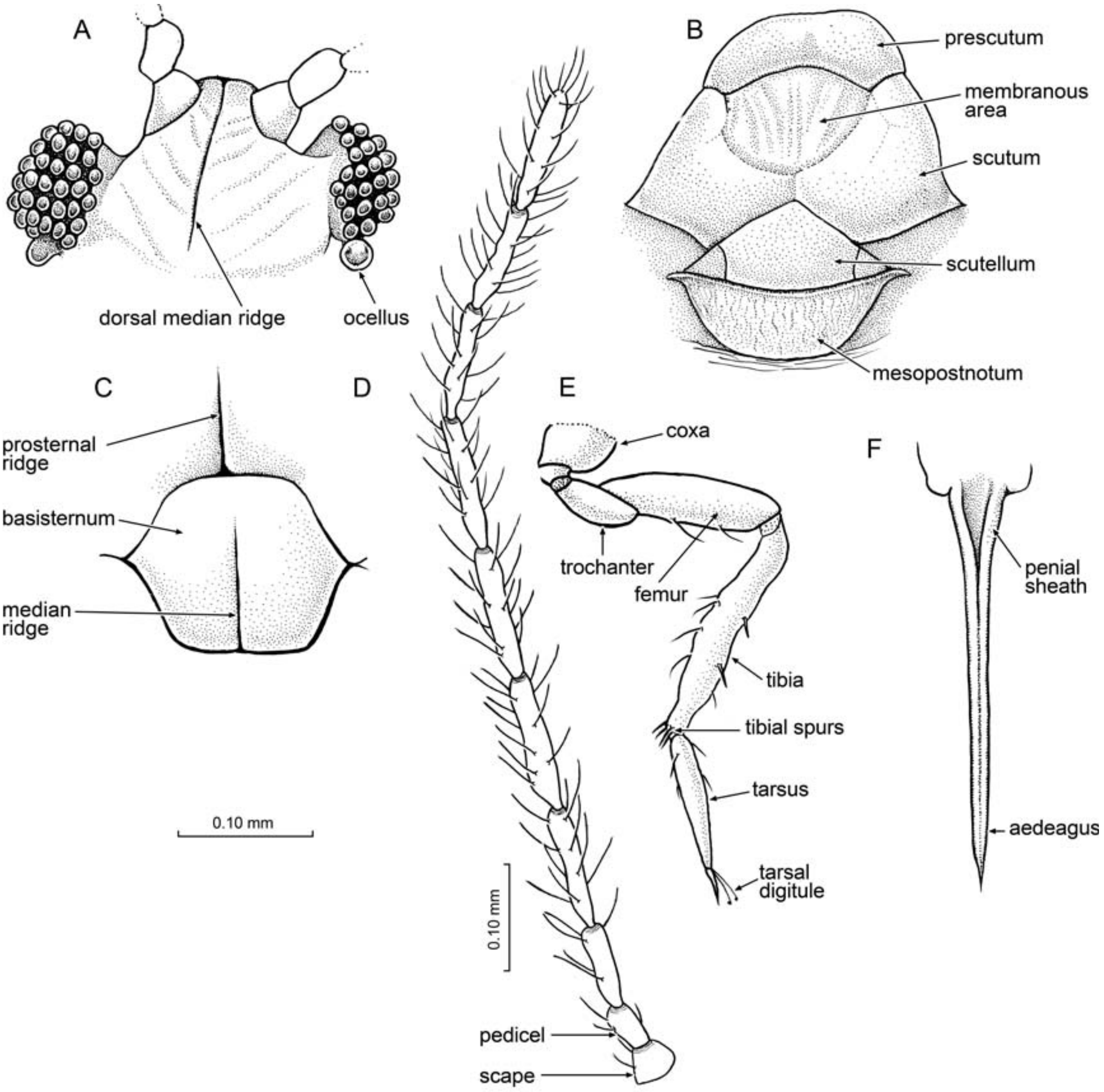


FIGURE 13. Details of *Xiphos vani,* n. sp. (**A**) Dorsal view of head. (**B**) Dorsal view of mesothorax. (**C**) Ventral view of pro- and mesothorax. (**D**) Antenna. (**E**) Leg. (**F**) Penial sheath.

femur, 38 µm wide, 150 µm long on proleg, with a few hairlike setae; tibia: 170 long µm, 25 µm wide, with hairlike setae becoming spinelike ventrally; tarsus 1-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** (fig. 13F): 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.

Alacrena, new genus

Type Species: *Alacrena peculiaris,* n. sp., by present designation and monotypy.

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

Etymology: The genus name comes from the Latin *ala*, meaning "wing," *crena*, meaning "notch," This refers to the notch found on the apex of the forewing. Gender: feminine.

Diagnosis: This genus is peculiar by the combination of the following characters: body minute, head large, compound eyes bulging, each with fewer than 100 ommatidia; antennal segments filiform, with capitate and fleshy setae on apical segment (vs. absent in archaeococcoids with compound eyes); wings hyaline, with a subcostal ridge extending to ¾ wing length, cubital ridge present ending at apical margin with a notch (vs. absent in all Coccoidea); hamulohalteres long and narrow; legs slender, tarsus 1-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.

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

The phylogenetic results retrieved *Alacrena* within the lineage including *Lebanococcus* and *Kozarius*, although the exact relationship remains unresolved. *Lebanococcus* and *Alacrena* share the presence of only subcostal and cubital ridges on the forewings, and the absence of tubular ducts. Despite the presence of well-developed compound eyes, *Lebanococcus* has a very different, telescopic abdomen (Koteja and Azar, 2008), shortened antennae, wings with a pterostigma and an anterior flexing patch, which are completely absent in *Alacrena*. The placement of *Alacrena* needs to be further investigated with additional, better preserved specimens (the unique specimen has all thoracic structures damaged). For now, the genus is considered incertae familiae.

Alacrena peculiaris, new species

Figures 12C, 14

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

Type: Holotype AMNH Bu-1516, alate male in a 5 × 4 × 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 the 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 male Coccoidea.

Diagnosis: As for genus.

Description: Body minute, total length 990 μm, largest width at mesothorax 200 μm. **Head** (fig. 14A): 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

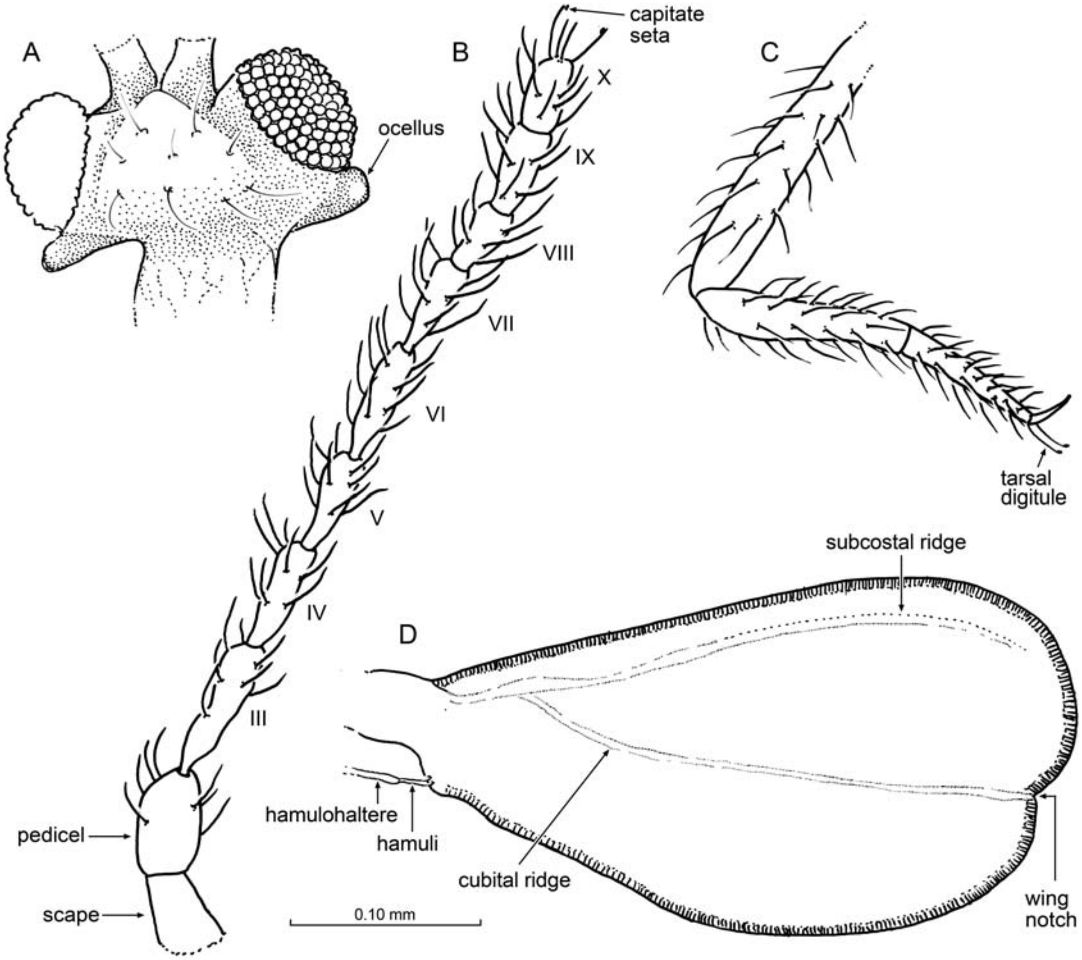


FIGURE 14. Details of *Alacrena peculiaris,* n. sp. (**A**) Dorsal view of head. (**B**) Antenna. (**C**) Leg from femur. (**D**) Forewing.

visible. **Antenna** (fig. 14B): 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 segments covered with 10–15 long hairlike setae (each 25-30 µm). Apical segment with hairlike setae, 2 capitate setae and at least 1 bristle. **Thorax:** Head and thorax separated by a neck constriction. All thoracic structures damaged, and not identifiable. **Wings** (fig. 14D): 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 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** (fig. 14C): 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 hairlike setae of same length as femur width; tibia: 155 µm long, 17 µm wide, with hairlike setae, tibial spurs not differentiated; tarsus 1-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 (fig. 13C). Aedeagus slender and pointed at apex. Eversible endophallus absent.

Magnilens, new genus

Type Species: *Magnilens glaesaria,* n. sp., by present designation and monotypy.

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

Etymology: The genus name comes from the Latin *magnus*, for "large," and *lens* 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 (vs. seven small ones in Putoidae, and six in *Solicoccus*, diagonally arranged); antenna filiform, almost trinodose (vs. not nodose in *Solicoccus*), with long setae; forewings with microtrichia; legs slender, tibia with setae becoming spinelike on ventral surface distally; tarsus 2-segmented; claw with spinelike digitules; abdominal segment VIII with a pair of wax filaments, indicative of a pair of glandular pouches (vs. two pairs of glandular pouches in *Solicoccus* on abdominal segments VII and VIII). Penial sheath large triangular, with a narrow pointed aedeagus (vs. long and bifurcated in Putoidae).

Species Included: *M. glaesaria,* n. sp.

Comments: *Magnilens* definitely belongs to the taxa bearing a row of multiple simple eyes. This genus seems most similar to Recent *Puto* with the following characters: the long antennal setae, the 2-segmented tarsus, with similar tibial spurs present ventrally and more numerous toward tarsus, presumable 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 bears very large and protruding eyes (vs. small round eyes in *Puto*), hamulohalteres bear two hamuli (vs. four hamuli), the tarsal digitules are undifferentiated (vs. differentiated), the claw denticles are absent (vs. present), the aedeagus is pointed apically (vs. bifurcated). The phylogenetic results based on morphological characters retrieved *Magnilens* as sister genus to *Solicoccus* (Labiococcidae) described in New Jersey amber (Koteja, 2000b) but not closely related to Putoidae. However, *Solicoccus* differs from *Magnilens* 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 one segment [VIII] in *Magnilens*), and three hamuli on the hamulohaltere (vs. two). Unfortunately, the specimen orientation does not allow a comparison of the thoracic structures, and until more specimens are found, *Magnilens* is considered incertae familiae.

Magnilens glaesaria, new species

Figures 15A, 16

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

Type: Holotype AMNH Bu-1418, alate male in a 4 × 7 × 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., deposited in the American Museum of Natural History.

Etymology: The epithet is from Latin *glaesum* to mean "of amber".

Diagnosis: As for genus.

Description: Body small, total length 1.37 mm long, widest width not measurable. **Head** (fig. 16A): Frontally flat ca. 290 µm wide, 140 µm long. Head structures not visible except for an ocular sclerite that surrounds head, each bearing seven pairs of large, protruding simple eyes. **Antenna** (fig. 16B): 10-segmented, total length 950 µm; segment lengths (in µm): scape ca. 45 µm long; pedicel, 80 µm long, with several 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. **Thorax:** Head and thorax separated by a narrow neck constriction. Prothorax membranous. Ridges on prothorax not observable. *Dorsally*: prescutum round and bulging anteriorly, other thoracic structures not clear. **Wings** (fig. 15A): 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 3/4 wing length. Cubital ridge 200 µm from wing base, extending to same level as subcostal ridge. Posterior flexing patch not observable Wing covered with microtrichia; alar setae present, sensoria not observed. Alar fold present. Hamulohalteres broad, each with two hamuli. **Legs** (fig. 16C): 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, with multiple tarsal spurs, tarsus 2-segmented, 160 µm long, and 20 µm wide, tarsal digitules absent; claw narrow almost straight, 30 µm long, claw digitule spinelike, 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 pouches laterally, each extruding two long wax filaments. **Genital segment** (fig. 16D): Penial sheath elongate triangular, about 245 µm long, with a few setae anteriorly. Aedeagus narrow, almost as long as penial sheath, pointed.

Pedicellicoccus, new genus

Type Species: *Pedicellicoccus marginatus,* n. sp., by present designation and monotypy.

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

Etymology: The genus name *Pedicellicoccus* is from the Latin *pedicellus*, diminutive of *pes*, "foot or pedicel" and refers to the enlarged and bulbous pedicel of this new genus. Gender: masculine.

Diagnosis: *Pedicellicoccus* differs from Electrococcidae and Pityococcidae by the combination of the following characters: body minute, head round and large relatively to body size (vs. relatively small), ocular sclerites each with apparently five or six pairs of simple eyes, arranged horizontally (vs. in a diagonally in Pityococidae), ventral eyes larger than lateral eyes (vs. of same size), not meeting medially (vs. not meeting medially in *Pityococcus* and *Turonicoccus*); antenna 9-segmented with an exceptionally enlarged pedicel (vs. not enlarged in Pityococcidae), heavily reticulated and with many short spinose setae; flagellar segments irregular in shape (vs. round), 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 (triangular, apically tapered and bifurcated); eversible endophallus present.

Species Included: *P. marginatus,* n. sp.

Comments: *Pedicellicoccus,* 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 *Pedicellicoccus*), head structures (eye rows arranged diagonally in *Pityococcus*, horizontally in *Pedicellicoccus*), and forewing shape (apically flat in *Pedicellicoccus*) all differ, including the extremely small size of *Pedicellicoccus*. The pedicel is extremely enlarged, which is known only in *Turonicoccus*, described in New Jersey amber (Koteja, 2000b). However, *Turonicoccus* has more nodose antennal segments, similar to *Pityococcus.* Our phylogenetic analysis retrieved *Pedicellicoccus* included in the clade comprising *Turonicoccus* and Pityococidae, although the relationship among these remains unresolved. *Turonicoccus* had been assigned to Electrococcidae (Koteja, 2000b) but *Electrococcus* and *Turonicoccus* were not retrieved as sister genera here. If *Turonicoccus* and *Pedicellicoccus* were considered to be in the family Pityococcidae, the morphological variation of this family would have to be expanded. Thus far, we consider *Pedicellicoccus* as a genus incertae familiae. This new fossil is among the smallest Coccoidea found in Burmese amber.

Pedicellicoccus marginatus, new species

Figures 15B–C, 17

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

Type: Holotype AMNH Bu-458 alate male; 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 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** (fig. 17A): Subrotund, 135 μm wide. Ocular sclerites well developed, each with at least 5 pairs of simple eyes (probably 6, but most dorsal eyes not visible because of specimen orientation). Ocelli not observed on specimen but probably present. **Antenna** (fig. 17A): 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 hairlike 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, scutum hidden by wings, scutellum suboval (rounded anterior margin) with an apparent median ridge (fig. 17B), ca. 40 μm long, 50 μm wide; mesopostnotum slightly longer than scutellum. *Ventrally*: basisternum 55 μm

FIGURE 15. Photomicrographs of (**A**) lateral view of *Magnilens glaesaria,* n. sp., holotype AMNH Bu-1418. (**B**) Dorsal and (**C**) ventral views of *Pedicellicoccus marginatus*, n. sp., holotype AMNH Bu-458.

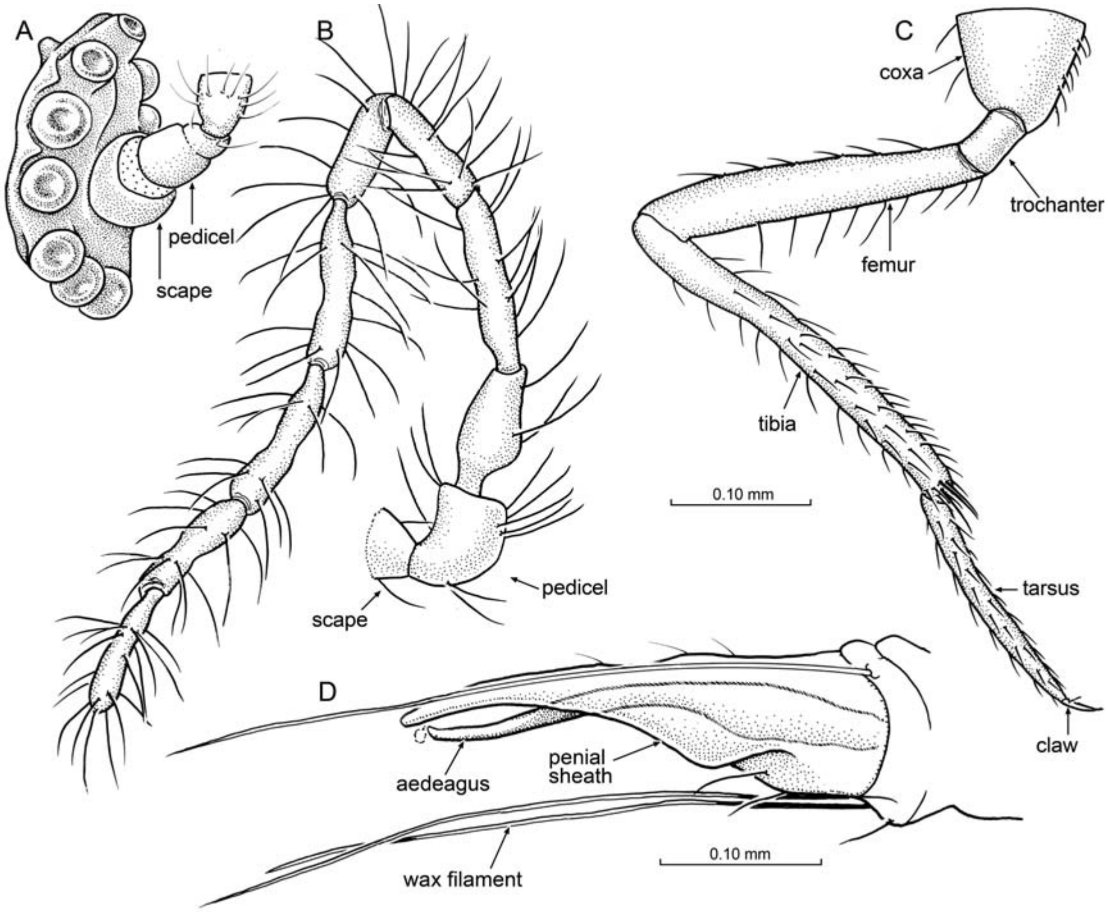


FIGURE 16. Details of *Magnilens glaesaria,* n. sp. (**A**) Head from lateral side. (**B**) Antenna. (**C**) Leg. (**D**) Penial sheath from lateral side.

long, 100 µm wide, with a basisternal median ridge; setae not observed. **Wings** (fig. 17C): 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 3/4 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** (fig. 17D): Small, of subequal length, cuticular reticulations absent; prothoracic legs: coxa not visible; trochanter and femur, ca. 90 µm long, ca.18 µm wide, with hairlike setae; tibia: 80 µm long, 20 µm wide, setae not visible; tarsus 1-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, with a pair of longer setae on segment VIII, glandular pouches not detected. **Genital segment** (fig. 17E): 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.

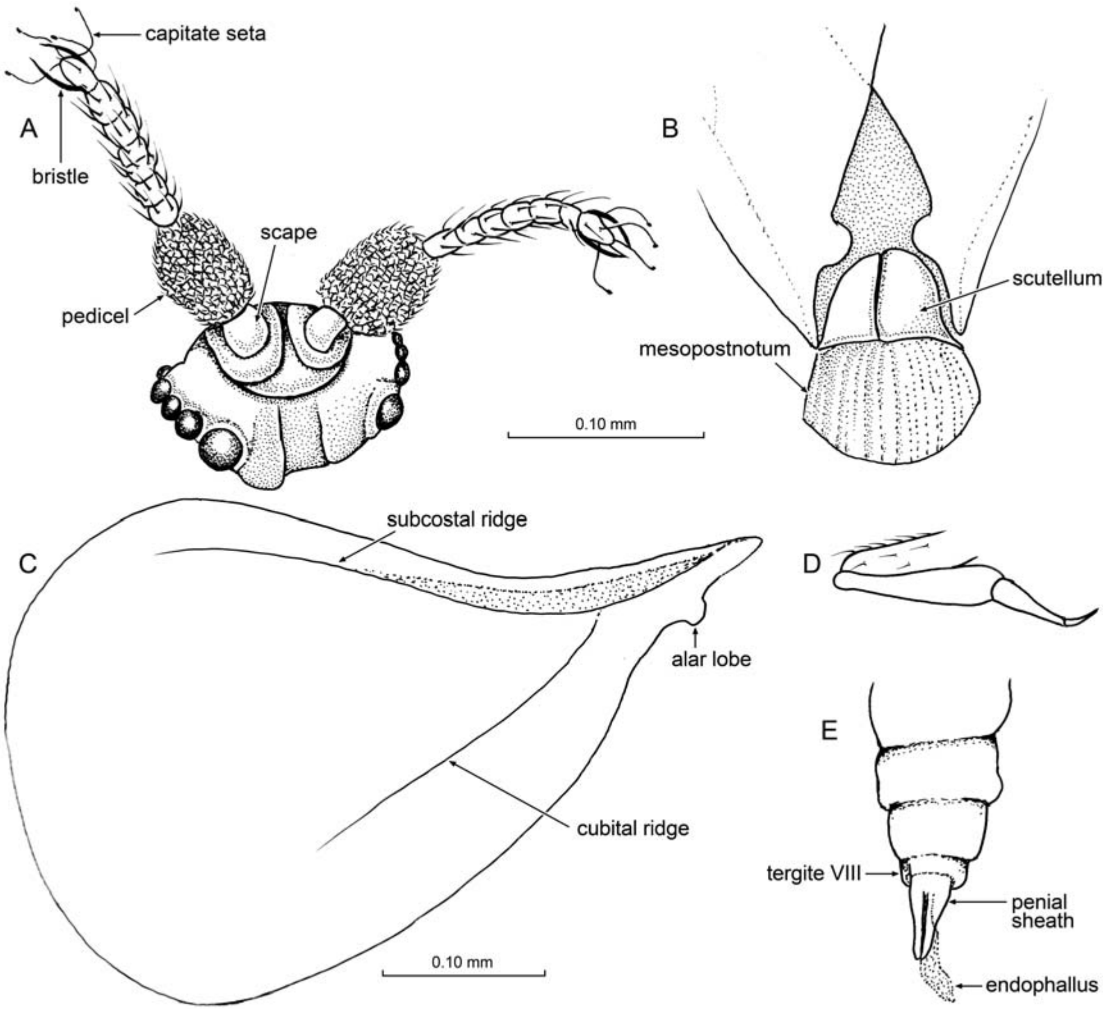


FIGURE 17. Details of *Pedicellicoccus marginatus,* n. sp. (**A**) Ventral view of head. (**B**) Dorsal view of mesothorax. (**C**) Wing. (**D**) Foreleg. (**E**) Posterior abdominal and genital segments.

Family Pseudococcidae Westwood, 1840

Williamsicoccus, new genus

Type Species: *Williamsicoccus megalops,* n. sp., by present designation and monotypy.

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

Etymology: The genus name is in tribute to Douglas Williams, for his tremendous contributions in scale insect systematics. Gender: masculine.

Diagnosis: Body minute, head constriction weak, not distinctively separated from prothorax, each ocular sclerite with a dorsal and a ventral simple 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; hamulohalteres long and thin, with one long hamulus; legs slender, each with one tibial spur; tarsus 2-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: *W. megalops,* n. sp.

Comments: *Williamsicoccus* is a neococcoid genus (it possesses two pairs of simple eyes) and was classified here within the family 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 of *Williamsicoccus* differ from *Ceroputo*; *Williamsicoccus* has a very narrow wing and has very large ventral eyes. *Williamsicoccus* also differs from *Gilderius,* 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 *Williamsicoccus* but round in *Gilderius*; the penial sheath is longer and the antennal setae are short in *Gilderius*. The phylogenetic analysis failed to retrieve *Williamsicoccus* as included within or related to the family Pseudococcidae (as well as any relationship with *Ceroputo*, which was sampled in the analysis). However, our analysis found *Gilderius* and *Williamsicoccus* to be sister genera, together a sister group to *Antonina*, a Pseudococcidae genus. This clade was found related to Recent families including Diaspididae, Cerococcidae, Aclerdidae, and Kerriidae. 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 *Williamsicoccus* in the family Pseudococcidae, and as such it is the oldest known fossil mealybug. (See Discussion section for *Pennygullania.*)

Williamsicoccus megalops, new species

Figures 18A–B, 19

Type Locality: Lebanon: Central Lebanon: Mdeyrij/Hammana: Caza Baabda: Mouhafazet Jabal Loubnon. Lower Cretaceous.

Type: Holotype 1582, alate male in a 4 × 4 × 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; Dany Azar amber collection, provisionally deposited in the Muséum National d'Histoire Naturelle.

Etymology: The epithet *megalops* comes from Greek *megalos*, meaning "large or great" and *ops*, "eye," referring to the large ventral eyes in this species and is a noun in apposition.

Diagnosis: As for genus.

Description: Body minute, total length 775 µm, widest at mesothorax, ca. 235 µm. **Head** (fig. 19AB): Round, ca. 210 µm wide, ca. 170 µm long. Each ocular sclerite with two 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). **Antenna** (fig. 19A): 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*: prescutum oval, bulging (85 µm wide, 72 µm long); scutum without a membranous area; scutellum oval, almost as wide as prescutum (fig. 19C). Setae not detected. *Ven-*

FIGURE 18. Photomicrographs of (**A**) dorsal and (**B**) ventral surfaces of *Williamsicoccus megalops,* n. sp., holotype 1582. (**C**) Dorsal and (**D**) ventral surfaces of *Gilderius eukrinops,* n. sp., holotype AMNH Bu-1594.

trally: basisternum well developed with a median ridge. **Wings** (fig. 19D): 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 3/4 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 (fig. 19E). **Legs** (fig. 19F): 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, hairlike setae; tibia: 130–160 µm long, 20 µm wide, with short hairlike setae, becoming numerous and spinose distally; tarsus 2-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 segmenta-

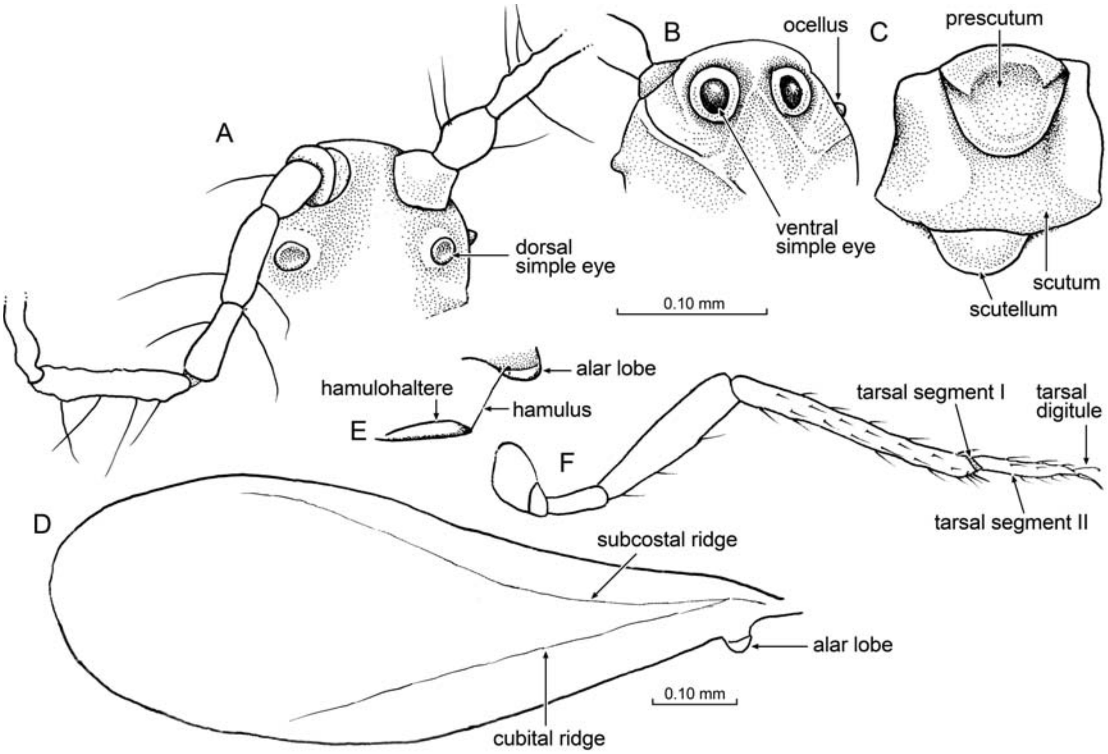


FIGURE 19. Details of *Williamsicoccus megalops,* n. sp. (**A**) Dorsal view of head. (**B**) Ventral view of head. (**C**) Dorsal mesothorax. (**D**) Wing. (**E**) Connection of the forewing and hamulohaltere. (**F**) Leg

tion 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.

Gilderius, new genus

Type Species: *Gilderius eukrinops,* n. sp., by present designation and monotypy.

Etymology: The genus was named after Richard Gilder, trustee of the American Museum of Natural History, for his major contribution in the creation of the Richard Gilder Graduate School. Gender: masculine.

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, not joining medially on both sides; antenna 10-segmented with setae shorter than segment width; basisternum without a median ridge; wings oval, hamulohalteres not visible; legs slender, tarsus 1-segmented, 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.

Comments: As in *Williamsicoccus,* n. gen., *Gilderius,* n. gen., with its two pairs of simple eyes and wax filaments protruding laterally from abdominal segments VII and VIII was 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 *Williamsicoccus*, see Comments section of *Williamsicoccus*.

Gilderius eukrinops, new species

Figures 18C–D, 20

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

Type: Holotype AMNH Bu-1594, alate male in a 3 × 4 × 1 yellow, transparent, polished amber piece with some debris; 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 the 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, and a noun in apposition.

Diagnosis: As for genus.

Description: Body small but robust, 840 µm long (body bent, true length probably nearer 900 µm), widest at mesothorax (ca. 300 µm wide). **Head** (fig. 20A): 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** (fig. 20B): 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. Hairlike setae shorter than segment width (setae ca. 20 µm long). Segment X with one short bristle and four 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 3/4 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** (fig. 20C): 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 hairlike setae; tibia: 155 µm long, 22 µm wide, with short hairlike setae, becoming more numerous and spinose distally; tarsus 1-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 posteriormost segments. Tergite VII and VIII each with a pair of long setae on each side. **Genital segment** (fig. 20D): Penial sheath subtriangular (130 µm long, 65 µm at base). Aedeagus slender and pointed at the apex. Eversible endophallus absent.

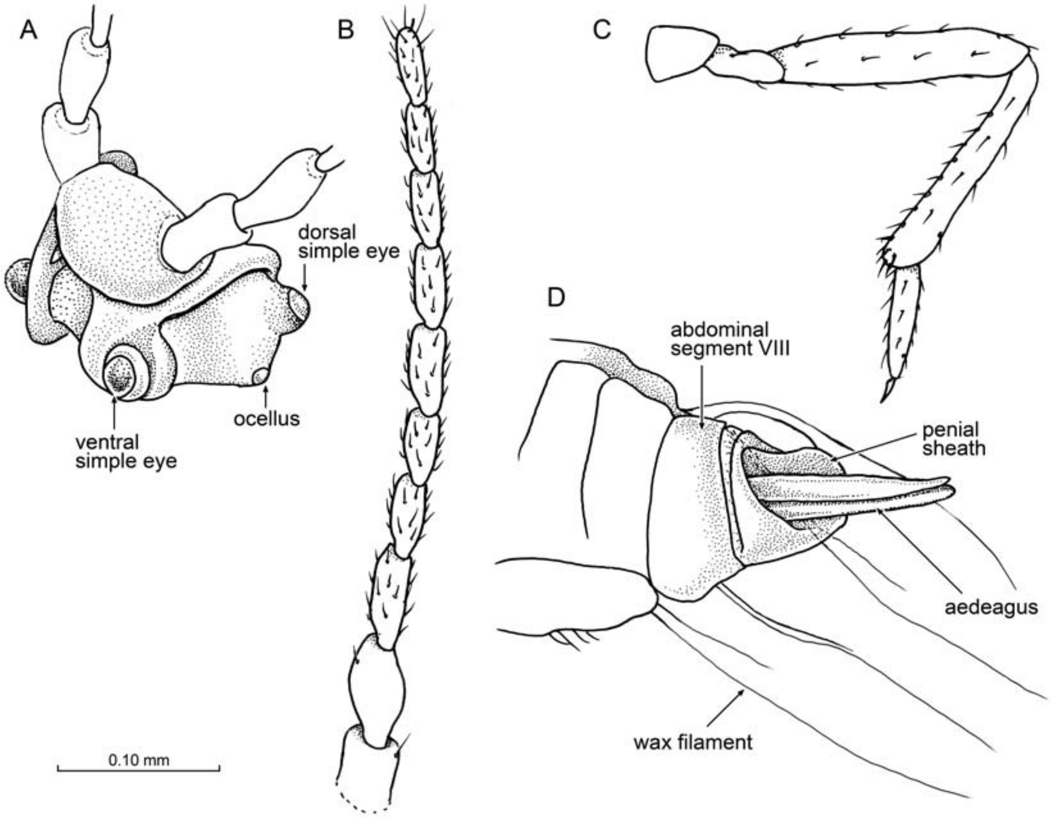


FIGURE 20. Details of *Gilderius eukrinops,* n. sp. (**A**) ventral view of head, (**B**) antenna, (**C**) leg, (**D**) dorsal view of penial sheath.

Family Coccidae Fallén, 1814

Rosahendersonia, new genus

Type Species: *Rosahendersonia prisca,* n. sp., by present designation and monotypy.

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

Etymology: The genus name is in tribute to the Late Rosa C. Henderson (1942–2012), 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.

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

Rosahendersonia as sister genus to the Coccidae. When 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.

Rosahendersonia prisca**,** new species

Figures 21A–B, 22

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

Type: Holotype AMNH Bu-835, alate male in a 7 × 5 × 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 the American Museum of Natural History.

Etymology: The epithet *prisca* is the feminine of Latin *priscus* meaning "belonging to former times, 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** (fig. 22A): Square shaped, 100 µm wide, 90 µm long. Dorsal head ridges (if present) obscured 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** (fig. 22D): 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 hairlike setae but flagellar segments (III to X) also bearing additional fleshy setae. All flagellar segments with hairlike setae as long as width of antennal segment (ca. 15 µm), but also with a pair of longer, hairlike setae (ca. 30 µm) on segments II–X. Apical segment with 4 long, capitate setae, 2 bristles, and 3–4 fleshy setae of same length as other shorter setae on flagellar segments. **Thorax** (fig. 22BC): 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 3/4 total wing length, with microtrichia. Alar setae and sensoria absent. Hamulohaltere absent. **Legs** (fig. 22E): 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 hairlike setae at least as long as tibial width, with a differentiated tibial spur, tarsus 1-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

FIGURE 21. Photomicrographs of (**A**) dorsal and (**B**) ventral surfaces of *Rosahendersonia prisca,* n. sp., holotype AMNH Bu-835. (**C**) Dorsal surface of *Normarkicoccus cambayae,* n. sp., holotype AMNH Tad-135.

µm widest, pleural setae present, with 3 or 4 longer setae on segment VIII, probably where glandular pouches are located. **Genital segment** (fig. 22F): Penial sheath subquadrate, short, with anterior half parallel sided, pointed apically, 72 µm long, 40 µm wide at base. Aedeagus thin and pointed.

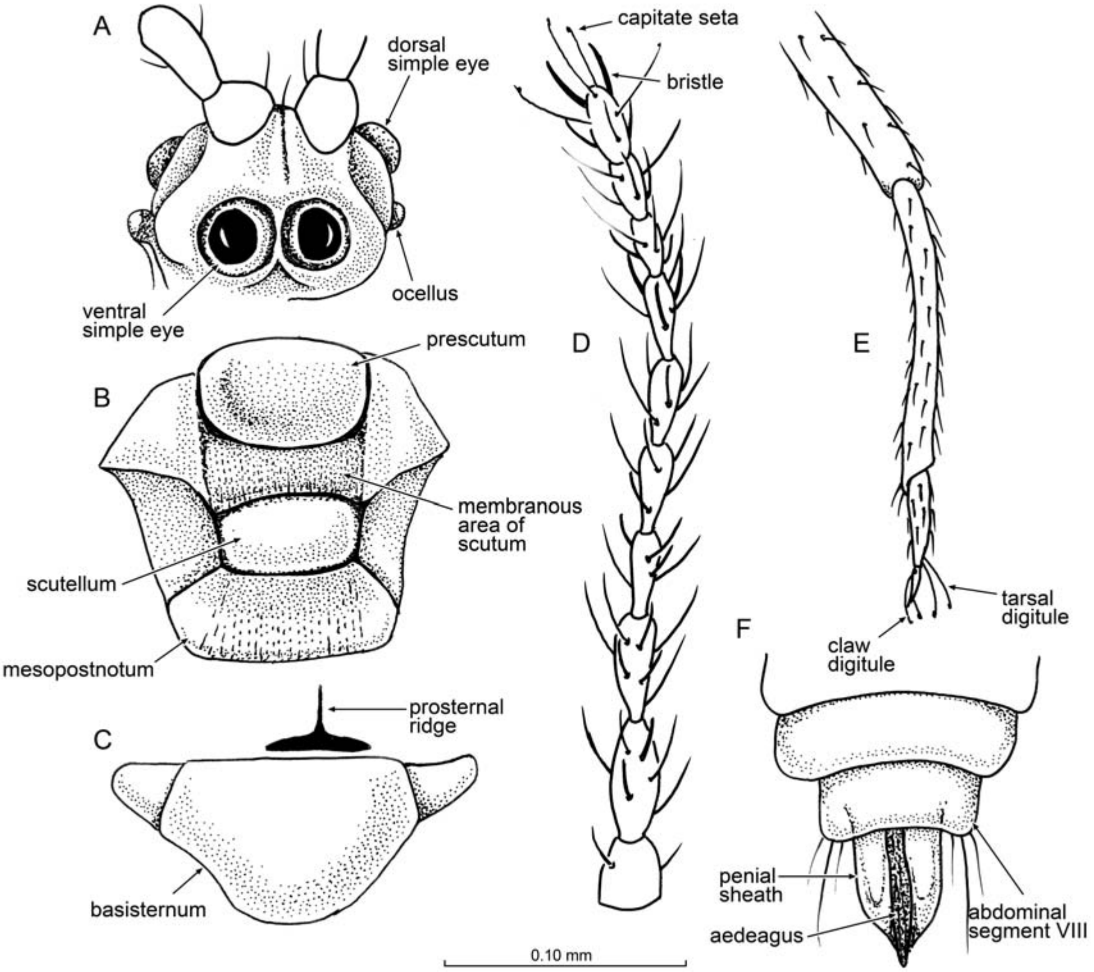


FIGURE 22. Details of *Rosahendersonia prisca,* n. sp. (**A**) Ventral view of head. (**B**) Dorsal view of mesothorax. (**C**) Ventral pro- and mesothorax. (**D**) Antenna. (**E**) Leg from femur. (**F**) Ventral view of abdominal segments VII and VIII and penial sheath.

Family Diaspididae Targioni Tozzetti, 1868

Normarkicoccus, new genus

TYPE SPECIES: *Normarkicoccus cambayae,* n. sp., by present designation and monotypy.

OCCURRENCE: India: Gujurat state, Tadkeshwar lignite mine near Surat (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, combined with the genus name *Coccus*. Gender: masculine.

DIAGNOSIS: Body minute, peared shaped, 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. cambayae,* n. sp.

Comments: This new genus was assigned to the Diaspididae based on the fused head and thorax, giving a general pear-shaped body; the forewing almost symmetrical on the anteroposterior axis and having an extremely reduced venation; thoracic structures almost unsclerotized; antennal shape, wherein the apical segment bears an apical seta; and the legs enlarged between tibia and tarsus. However, the absence of elongate and needlelike penial sheath and 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, in order to reach the vulva, inserts under the hard cover or test (pupal cover) secreted by the female. 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, *Normarkicoccus* is not retrieved within the Diaspididae, but is a sister group to the lineage including Cerococcidae, Aclerdidae, and Kerriidae. The Diaspididae is well supported, for instance, by the presence of a long, spinelike penial sheath and by the presence of antennal capitate setae, features that are absent in *Normarkicoccus.* Additionally, due to the specimen preservation, the amount of missing data could have led to our phylogenetic results. Additional character coding of features focusing on the Diaspididae, should provide a better understanding of the relationships of this fossil genus.

Normarkicoccus cambayae, new species

Figures 21C, 23

Type Locality: Early Eocene, India, Gujarat, western India: Tadkeshwar lignite mines.

Type: Holotype Tad-135, alate male in a 4 × 5 × 0.5 mm dark orange, polished amber piece, specimen in relatively good condition but with thoracic structures damaged, wings spread backward and touching together, body tilted in amber; accessible views: partial ventral and dorsal. India: Gujarat, 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.

Etymology: The species epithet comes from Cambay, the geological basin from which the amber was excavated.

Diagnosis: As for genus.

Description: Body minute, spindle shaped, total length 365 µm, widest at mesothorax (ca. 200 µm). **Head** (fig. 23AB): 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 hairlike 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 hairlike 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 2 longer and thinner setae; 1 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, symmetri-

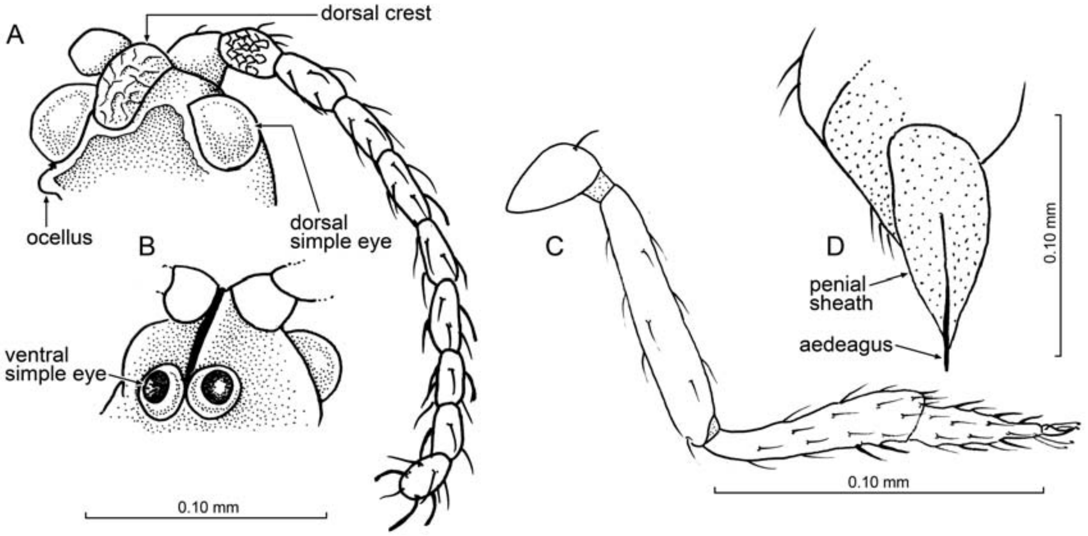


FIGURE 23. Details of *Normarkicoccus cambayae,* n. sp. (**A**) Dorsal view of head. (**B**) Ventral view of head. (**C**) Leg. (**D**) Ventral view of penial sheath.

cal on midlongitudinal axis; subcostal ridge extending from base of the wing to more than 3/4 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** (fig. 23C): 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 hairlike setae (ca. 15 µm long); tibia 155 µm long, proximally narrow (7 µm wide), distally twice the basal width, with a few hairlike setae, more numerous and spinose distally (tibial spurs); tarsus 2-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** (fig. 23D): 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.

PHYLOGENETIC RESULTS

A total of 174 morphological characters were coded for all Recent taxa (except in a few cases where only male characters were coded, e.g., *Phenacoleachia*) and all fossils had only macropterous males coded. The morphological matrix is available at Morphobank (O'Leary and Kaufman, 2012) under Project 1013 (http://www.morphobank.org/index.php/MyProjects/List/select/project_id/1013). The percentage of coded characters is summarized in the appendix. The MP analysis using TNT and including 64 Recent taxa, 43 fossil terminals and five outgroups, retrieved 32 most parsimonious trees (MPT) of 1872 steps (fig. 24A–C). Coccoidea is found to be monophyletic (node "a") and defined by males in which mouthparts are absent, the membranous mesothorax, one pretarsal claw, and the absence of true ocelli in macropterous males. All Recent families with more than one terminal were retrieved as monophyletic except for Pseudococcidae, with *Antonina* retrieved in a clade of fossil taxa (fig. 24C). As currently recognized, the family Eriococcidae is paraphyletic (but see Cook et al., 2002). The fossil family Jersicoccidae was retrieved as sister group to the remaining Coccoidea, followed by Matsucoccidae, then Ortheziidae.

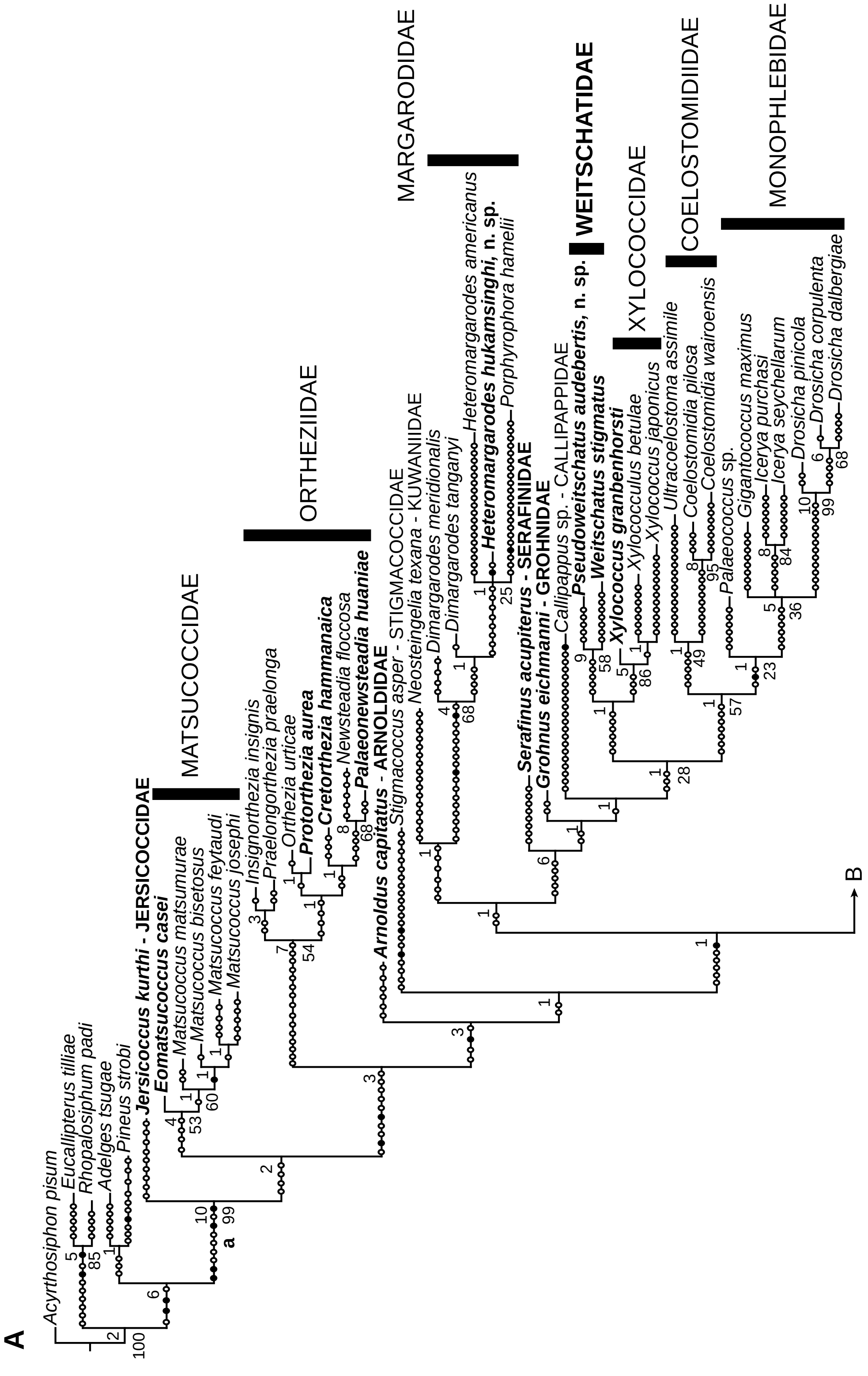
Families grouped into the "archaeococcoid" lineage were found to be paraphyletic, consistent with previous phylogenetic studies based on morphological data (e.g., Hodgson and Foldi, 2005; Hodgson and Hardy, 2013). Fossils originally identified as Margarodidae, Matsucoccidae, and Ortheziidae were placed within their respective families. Xylococcidae and xylococcid-like fossil families (Arnoldidae, Grohnidae, Serafinidae, Weitschatidae) were found to be paraphyletic and scattered among different locations: Weitschatidae as sister group to Recent Xylococcidae. Serafinidae and Grohnidae are successively sister groups to the lineage including Recent Callipappidae, Xylococcidae, Coelostomidiidae, and Monophlebidae. Finally, Arnoldidae is retrieved as sister to all Coccoidea except Matsucoccidae, Ortheziidae, and Jersicoccidae. The new Cretaceous genus *Xiphos*, although similar to xylococcid-like taxa was retrieved in a lineage including Burmacoccidae, Lebanococcidae, the new family Kozariidae, and new genus *Alacrena*. The new Cretaceous family Kozariidae was retrieved as the sister group to two Cretaceous taxa *Alacrena* and Lebanococcidae, although the basal relationship is not resolved.

Figure 23B shows lineages in which males do not possess compound eyes. This includes an undescribed fossil inclusion in French amber (ARC 60.1), Hodgsonicoccidae, *Palaeotupo*, a lineage including Recent families Steingeliidae, Phenacoleachiidae, and Putoidae, fossil *Magnilens* + *Solicoccus*, a lineage including fossil *Electrococcus*, Grimaldiellidae, *Pedicellicoccus*, *Turonicoccus* and Recent Pityococcidae, fossil Kukaspididae, and Apticoccidae. These fossil taxa originate from amber deposits around the world, and thus reveal a much larger diversity of lineages where males bore a row of multiple simple eyes, now represented by only a few species in the Recent fauna (Steingeliidae, Putoidae, Phenacoleachiidae, and Pityococcidae).

The Recent neococcoids is retrieved as a monophyletic lineage in this analysis. However, when considering fossils, *Albicoccus* is included in the neococcoid lineage, contrary to Koteja (2004). Additionally, in considering node "b", this clade includes Recent neococcoids, in addition to three fossil genera: *Kuenowicoccus, Pennygullania,* and *Inka*. *Kuenowicoccus* was described as an eriococcid male (Koteja, 1988c), but is not retrieved as related to any of the sampled genera recognized as Eriococcidae. *Pennygullania,* and *Inka* were described and assigned to two new families (Koteja 2008; Koteja and Poinar, 2001), and considered as neococcoids. Other fossils included in the neococcoid lineage are *Marmyan* from Burmese amber, retrieved as sister group to *Eriococccus* and Pseudococcidae (excluding *Antonina*), *Rosahendersonia*, found as the sister group to Recent sampled Coccidae, a lineage including Albicoccidae, Recent *Antonina*, and the new fossil *Gilderius* and *Williamsicoccus*, identified as Pseudococcidae in our study. Finally, *Normarkicoccus,* identified as a fossil Diaspididae was retrieved as sister to Cerococcidae + Aclerdidae + Kerriidae.

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


A
Acyrthosiphon pisum
Eucallipterus tilliae
Rhopalosiphum padi
Adelges tsugae
Pineus strobi
Jersicoccus kurthi - JERSICOCCIDAE
Eomatsucoccus casei
Matsucoccus matsumurae
Matsucoccus bisetosus
Matsucoccus feytaudi
Matsucoccus josephi
MATSUCOCCIDAE
Insignorthezia insignis
Praelongorthezia praelonga
Orthezia urticae
Protorthezia aurea
Cretorthezia hammanaica
Newsteadia floccosa
Palaeonewsteadia huaniae
ORTHEZIIDAE
Arnoldus capitatus - ARNOLDIDAE
Stigmacoccus asper - STIGMACOCCIDAE
Neosteingelia texana - KUWANIIDAE
Dimargarodes meridionalis
Dimargarodes tanganyi
Heteromargarodes americanus
Heteromargarodes hukamsinghi, n. sp.
Porphyrophora hamelii
MARGARODIDAE
Serafinus acupiterus - SERAFINIDAE
Grohnus eichmanni - GROHNIDAE
Callipappus sp. - CALLIPAPPIDAE
Pseudoweitschatus audebertis, n. sp.
Weitschatus stigmatus
WEITSCHATIDAE
Xylococcus granbenhorsti
Xylococculus betulae
Xylococcus japonicus
XYLOCOCCIDAE
Ultracoelostoma assimile
Coelostomidia pilosa
Coelostomidia wairoensis
COELOSTOMIDIIDAE
Palaeococcus sp.
Gigantococcus maximus
Icerya purchasi
Icerya seychellarum
Drosicha pinicola
Drosicha corpulenta
Drosicha dalbergiae
MONOPHLEBIDAE
B
a
5
85
1
2
100
6
10
99
2
4
53
1
1
60
1
3
3
7
54
1
1
1
8
68
3
1
1
1
1
4
68
1
1
25
6
1
1
9
58
1
5
86
1
1
28
1
49
8
95
1
57
1
23
5
36
8
84
10
99
6
68

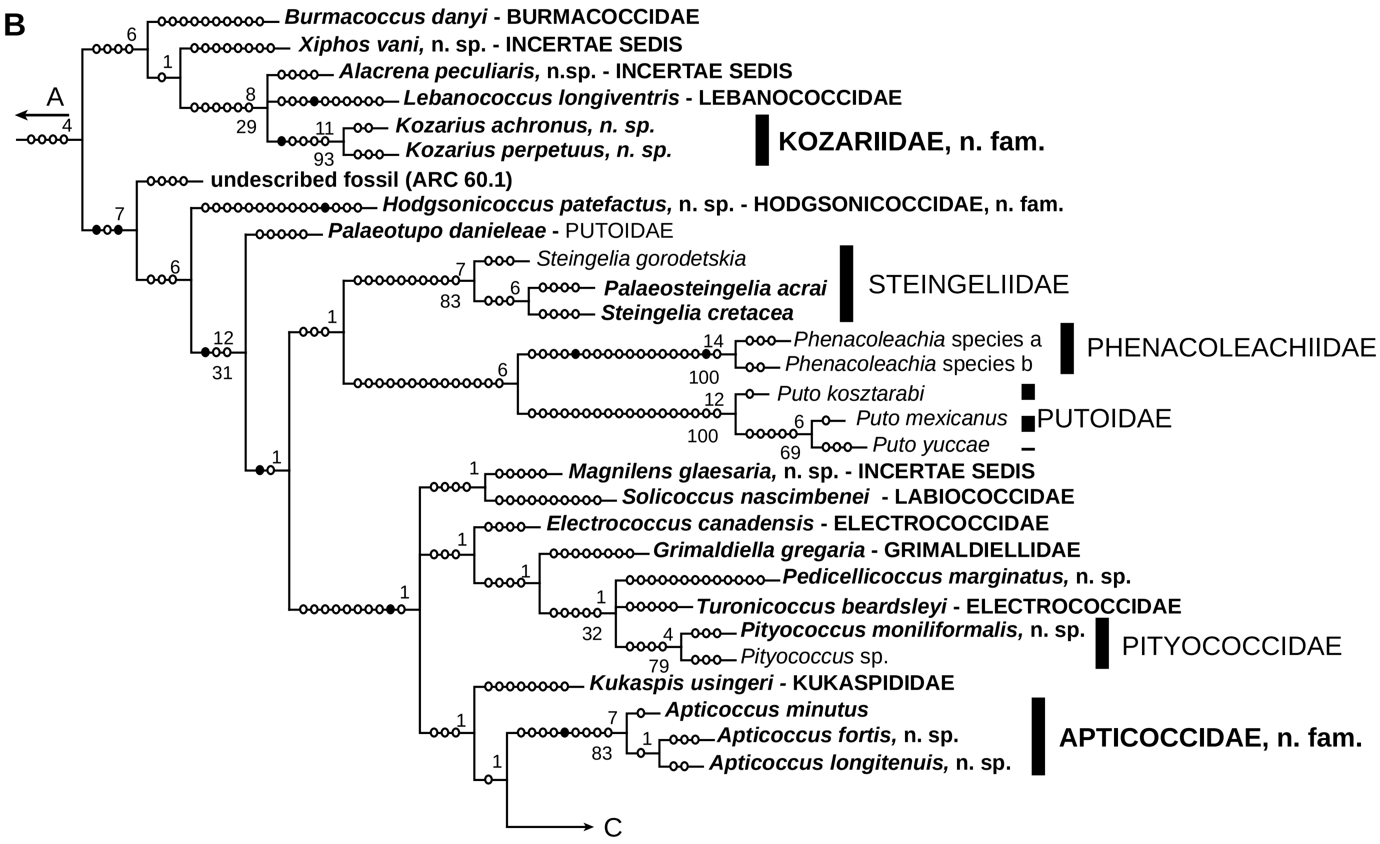
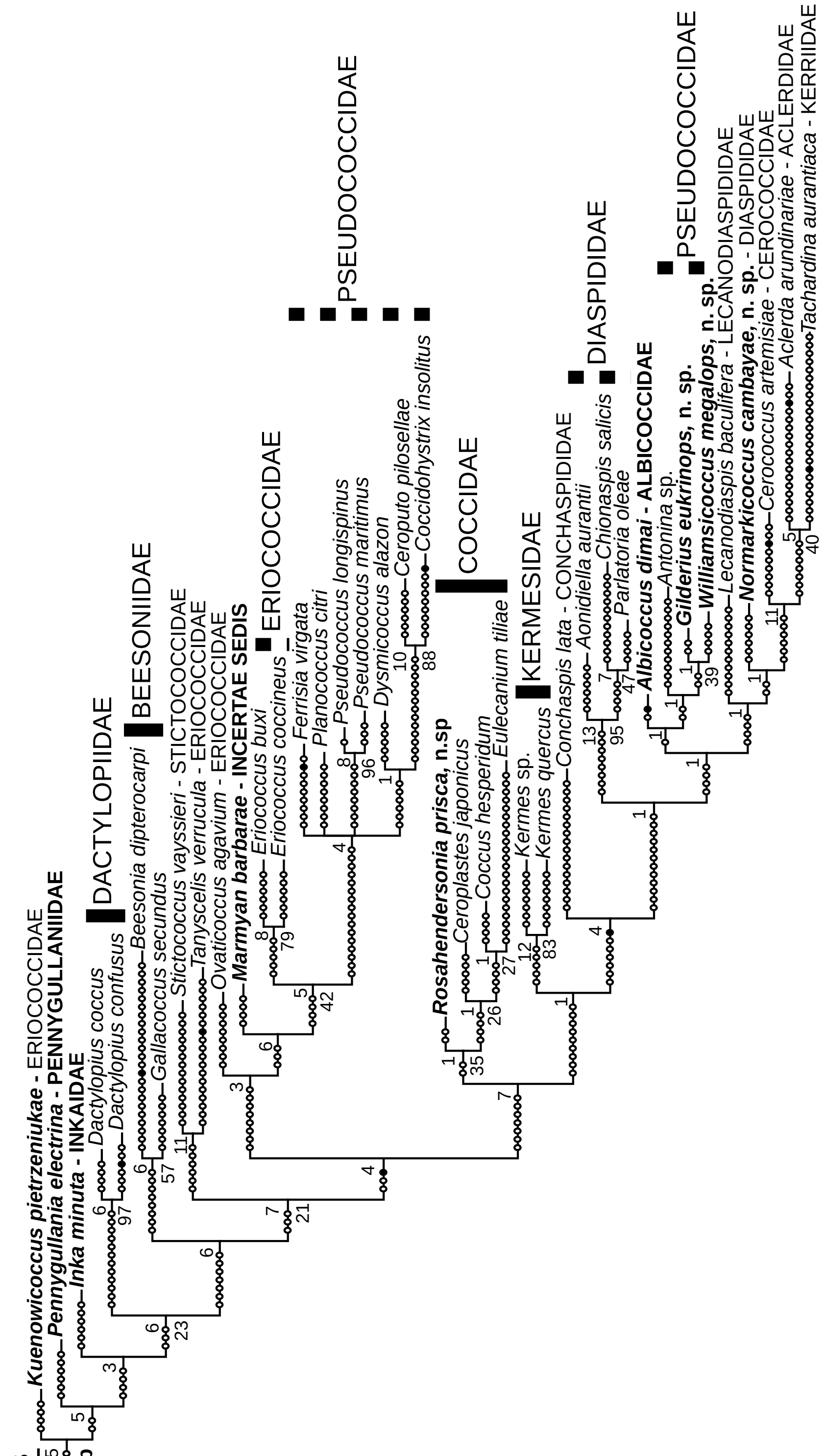


FIGURE 24. Strict consensus of the 32 most parsimonious trees retrieved from TNT using 112 taxa (fossil + Recent) and 174 morphological characters. The tree is divided into three parts, A (opposite page), B (above), and C (next page). Fossil taxa are represented in bold. Unambiguous characters were mapped as dots on branches with, black dots = unique change, white dots = multiple changes. Branch supports are indicated above branches for Bremer and below branches for jackknife supports (below) >20 (P = 36).


C
B
b
Kuenowicoccus pietrzeniukae - ERIOCOCCIDAE
Pennygullania electrina - PENNYGULLANIIDAE
Inka minuta - INKAIDAE
Dactylopius coccus
Dactylopius confusus
DACTYLOPIIDAE
Beesonia dipterocarpi
BEESONIIDAE
Gallacoccus secundus
Stictococcus vayssieri - STICTOCOCCIDAE
Tanyscelis verrucula - ERIOCOCCIDAE
Ovaticoccus agavium - ERIOCOCCIDAE
Marmyan barbarae - INCERTAE SEDIS
Eriococcus buxi
Eriococcus coccineus
ERIOCOCCIDAE
Ferrisia virgata
Planococcus citri
Pseudococcus longispinus
Pseudococcus maritimus
Dysmicoccus alazon
Ceroputo pilosellae
Coccidohystrix insolitus
PSEUDOCOCCIDAE
Rosahendersonia prisca, n.sp
Ceroplastes japonicus
Coccus hesperidum
Eulecanium tiliae
COCCIDAE
Kermes sp.
Kermes quercus
KERMESIDAE
Conchaspis lata - CONCHASPIDIDAE
Aonidiella aurantii
Chionaspis salicis
Parlatoria oleae
DIASPIDIDAE
Albicoccus dimai - ALBICOCCIDAE
Antonina sp.
Gilderius eukrinops, n. sp.
Williamsicoccus megalops, n. sp.
PSEUDOCOCCIDAE
Lecanodiaspis baculifera - LECANODIASPIDIDAE
Normarkicoccus cambayae, n. sp. - DIASPIDIDAE
Cerococcus artemisiae - CEROCOCCIDAE
Aclerda arundinariae - ACLERDIDAE
Tachardina aurantiaca - KERRIIDAE
5
5
5
3
6
23
6
97
6
57
6
11
7
21
4
3
6
8
79
5
42
4
8
96
1
10
88
7
1
35
1
26
1
27
12
83
1
4
13
95
7
47
1
1
1
1
1
39
1
1
1
11
5
40

described a total of 16 new species in 14 genera (11 of them new) and nine families (three of them new). The amber from the Cretaceous Period provided most of the new specimens as well as most of the new diversity. Figure 25 (accompanied with table 1) is an updated summary of the coccoid fossil record at the family level, highlighting the many new records made by this study. Lebanese amber now contains more families (10) than any other Cretaceous deposit, followed by Burmese (6) and New Jersey (7), although there are 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/Bitterfield ambers (Eocene) preserve more fossilized coccoids—in 15 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 19 extinct families of Coccoidea (five of them in Eocene Baltic amber, the 14 others from Cretaceous deposits (Canada, 1; Taymir, 1, New Jersey, 4; Alaska, 1; Burmese, 2; Lebanese, 5). Of the 32 Recent coccoid families, 13 are represented in the fossil record, seven of which are known only from the Eocene and Oligocene (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 among the most successful archaeococcoid 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.

Several xylococcid-like taxa were described from Baltic amber but classified into several new families: Arnoldidae, Serafinidae, Weitschatidae, and Grohnidae (Koteja, 2008). Koteja based his generic diagnosis of Xylococcidae on Morrison (1928), in which the tribe Xylococcini was defined by the presence of a radial sector on the forewing. On 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 only comprises two Recent genera (*Xylococcus* Löw and *Xylococculus* Morrison), which are so uniform that Hodgson and Foldi (2006) do not even consider their male morphological differences sufficient to warrant their placement in separate genera. Table 2 presents a comparison of key characters among xylococcid-like genera, including *Pseudoweitschatus,* n. gen., and *Xiphos,* n. gen. (assigned for now as incertae sedis). Fossil xylococcid-like taxa were certainly much more diverse, even as late as 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, except for the close relationship of Xylococcidae with Weitschatidae.

We also described from the same Cambay deposit a new putative Diaspididae genus, *Normarkicoccus,* n. gen. Although general morphology suggests an assignment to the Diaspididae, the genus has a short penial sheath, unlike its Recent counterparts. Moreover, our phylogenetic hypothesis did not retrieve *Normarkicoccus* related to Recent sampled Diaspididae. Diaspididae are probably the most derived members of Coccoidea, in which females generally completely lost

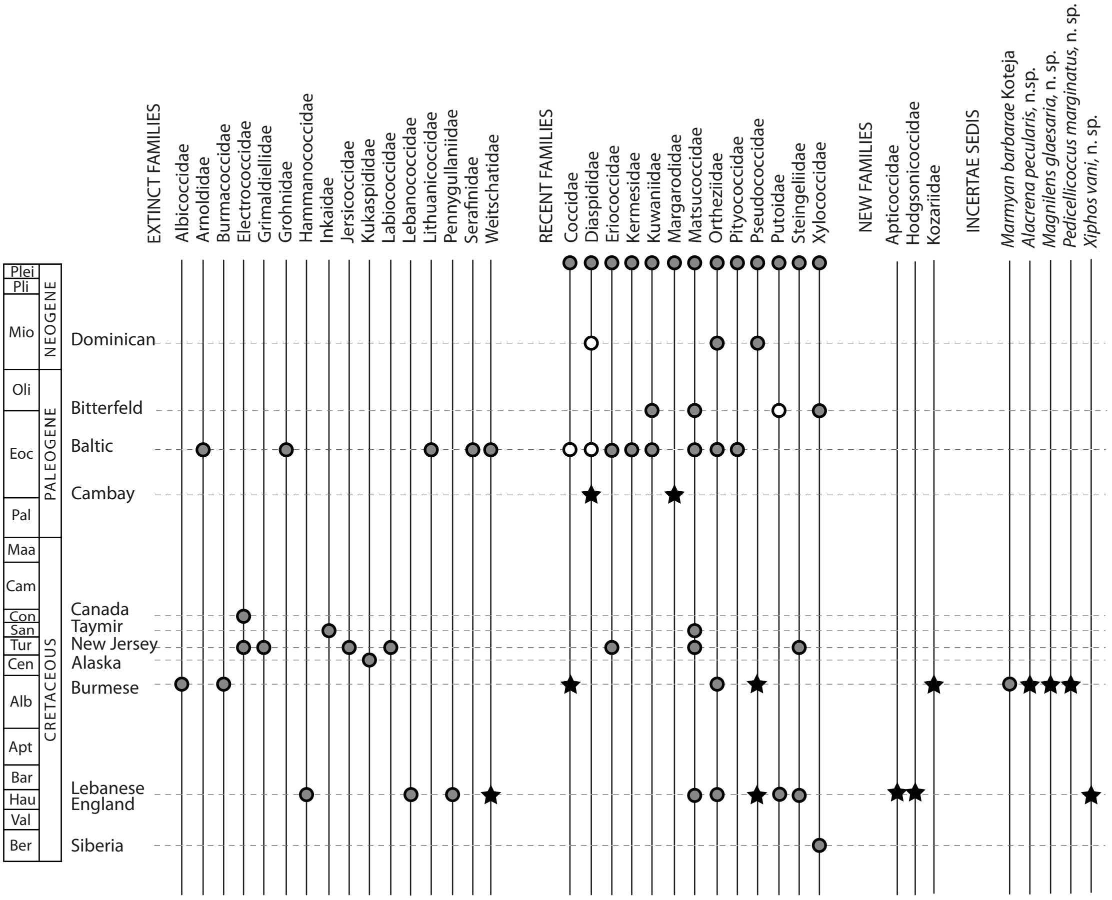


FIGURE 25. Diagram summarizing known fossil scale insects for each fossil deposit. Symbols indicates: grey circle = previously described taxa; dark star = herein described; white circle = undescribed.

TABLE 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.

Family	Genus	Species	Deposit	Reference(s)	Life stage
†Albicoccidae	†*Albicoccus*	*dimai* Koteja	Bu	Koteja, 2004	Macropterous male
†Apticoccidae	†*Apticoccus*	***fortis*** **Vea and Grimaldi**	Le	Herein	Macropterous male
		minutus Koteja and Azar	Le	Koteja and Azar, 2008	Macropterous male
		longitenuis **Vea and Grimaldi**	Le	Herein	Macropterous male
†Arnoldidae	†*Arnoldus*	*capitatus* Koteja	Ba	Koteja, 2008	Macropterous male
		clavatus Koteja	Ba	Idem	Macropterous male
†Burmacoccidae	†*Burmacoccus*	*danyi* Koteja	Bu	Koteja, 2004	Macropterous male

Family	Genus	Species	Deposit	Reference(s)	Life stage
Coccidae	**†*Rosahendersonia***	***prisca* Vea and Grimaldi**	Bu	Herein	Macropterous male
Diaspididae	**†*Normarkicoccus***	***cambayae* Vea and Grimaldi**	Cb	Herein	Macropterous male
†Electrococcidae	†*Electrococcus*	*canadensis* Beardsley	Ca	Beardsley, 1969	Macropterous male
	†*Turonicoccus*	*bearsdleyi* Koteja	NJ	Koteja, 2000b	Macropterous male
		grimaldii Koteja	NJ	Idem	Macropterous male
Eriococcidae	†*Balticococcus*	*oblicus* Koteja	Ba	Koteja, 1988b	First instar nymph
		spinosus Koteja	Ba	Idem	First instar nymph
	†*Gedanicoccus*	*gracilis* Koteja	Ba	Idem	First instar nymph
	†*Jutlandicoccus*	*pauper* Koteja	Ba	Idem	First instar nymph
		perfectus Koteja	Ba	Idem	First instar nymph
	†*Koteya*	*luzzii* Koteja	NJ	Koteja, 2000b; Özdikmen, 2011	Second instar nymph
	†*Kueniwococcus*	*pietrzeniukae* Koteja	Ba	Koteja, 1988c	Macropterous male
†Grimaldiellidae	†*Grimaldiella*	*gregaria* Koteja	NJ	Koteja, 2000b	Macropterous male
		resinophila Koteja	NJ	Idem	Macropterous male
†Grohnidae	†*Grohnus*	*eichmanni* Koteja	Ba	Koteja, 2008	Macropterous male
†Hammanococcidae	†*Hammanococcus*	*setosus* Koteja and Azar	Le	Koteja and Azar, 2008	Macropterous male
		sp. Koteja and Azar	Le	Idem	Instar nymph
†Hodgsonicoccidae	**†*Hodgsonicoccus***	***patefactus* Vea and Grimaldi**	Le	Herein	Macropterous male
†Inkaidae	†*Inka*	*minuta* Koteja	Ta	Koteja, 1989b	Macropterous male
†Jersicoccidae	†*Jersicoccus*	*kurthi* Koteja	NJ	Koteja, 2000b	Macropterous male
Kermesidae	†*Sucinikermes*	*kulickae* Koteja	Ba	Koteja, 1988d	First instar nymph
†Kozariidae	**†*Kozarius***	***achronus* Vea and Grimaldi**	Bu	Herein	Macropterous male
		***perpetuus* Vea and Grimaldi**	Bu	Herein	Macropterous male
†Kukaspiidae	†*Kukaspis*	*usingeri* Koteja and Poinar	Al	Koteja and Poinar, 2001	Macropterous male
Kuwaniidae	†*Hoffeinsia*	*foldii* Koteja	Ba+Bi	Koteja, 2008	First instar nymph
†Labiococcidae	†*Labiococcus*	*joosti* Koteja	NJ	Koteja, 2000b	First instar nymph
	†*Solicoccus*	*nascimbenei* Koteja	NJ	Idem	Macropterous male
†Lebanococcidae	†*Lebanococcus*	*longiventris* Koteja and Azar	Le	Koteja and Azar, 2008	Macropterous male
†Lithuanicoccidae	†*Lithuanicoccus*	*damzeni* Koteja	Ba	Koteja, 2008	Apterous adult male
		kozmowskae Koteja	Ba	Idem	
Margarodidae	*Heteromargarodes*	***hukamsinghi* Vea and Grimaldi**	Cb	Herein	Macropterous male
Matsucoccidae	†*Eomatsucoccus*	*andrewi* Koteja	En	Koteja, 1999	Macropterous male
		casei Koteja	NJ	Koteja, 2000b	Macropterous male
		popovi Koteja	Ta	Koteja, 1988a	Macropterous male
		sukachevae Koteja	Ta	Idem	Macropterous male
	Matsucoccus	*apterus* Koteja	Ba	Koteja, 1984	Macropterous male
		electrinus Koteja	Ba	Idem	Macropterous male
		larssoni Koteja	Ba	Idem	Macropterous male
		saxonicus Koteja	Bi	Koteja, 1986b	Macropterous male

Family	Genus	Species	Deposit	Reference(s)	Life stage
Ortheziidae	*Arctorthezia*	*antiqua* Koteja	Ba	Koteja and Zak-Ogaza, 1988a	Adult female
		baltica Vea and Grimaldi	Ba	Vea and Grimaldi, 2012	Last instar nymph
	†*Burmorthezia*	*insolita* Vea and Grimaldi	Bu	Vea and Grimaldi, 2012	Last instar nymph
		kotejai Vea and Grimaldi	Bu	Idem	Last instar nymph
	†*Cretorthezia*	*hammanaica* Koteja and Azar	Le	Koteja and Azar, 2008	Macropterous male
	Mixorthezia	*dominicana* Vea and Grimaldi	DR	Vea and Grimaldi, 2012	Last instar nymph
		kozari Vea and Grimaldi	DR	Idem	Adult female
	Newsteadia	*succini* Koteja and Zak-Ogaza	Ba	Koteja and Zak-Ogaza, 1988b	Adult female
	†*Palaeonewsteadia*	*huaniae* Koteja	Ba	Koteja,1987a	Macropterous male
	†*Protorthezia*	*aurea* Koteja	Ba	Koteja, 1987b	Macropterous male
†Pennygullaniidae	†*Pennygullania*	*electrina* Koteja and Azar	Le	Koteja and Azar, 2008	Macropterous male
Pityococcidae	†*Cancerococcus*	*apterus* Koteja	Ba	Koteja, 1988c; Miller and Gimpel, 1999 for classification	Apterous adult male
	Pityococcus	***moniliformalis* Vea and Grimaldi**	Ba	Herein	Macropterous male
Pseudococcidae	†*Electromyrmecoccus*	*abductus* Williams	DR	Johnson et al. 2001	Adult female
		inclusus Williams and Agosti	DR	Johnson et al., 2001	Adult female
		reginae Williams	DR	Johnson et al., 2001	Adult female
	†*Gilderius*	***eukrinops* Vea and Grimaldi**	Bu	Herein	Macropterous male
	†*Williamsicoccus*	***megalops* Vea and Grimaldi**	Le	Herein	Macropterous male
Putoidae	†*Palaeotupo*	*danieleae* Koteja and Azar	Le	Koteja and Azar, 2008	Macropterous male
†Serafinidae	†*Serafinus*	*acupiterus* Koteja	Ba	Koteja, 2008	Macropterous male
Steingeliidae	†*Palaeosteingelia*	*acrai* Koteja and Azar	Le	Koteja and Azar, 2008	Macropterous male
		caudata Koteja and Azar	Le	Idem	Macropterous male
	Steingelia	*cretacea* Koteja	NJ	Koteja, 2000b	Macropterous male
†Weitschatidae	†*Weitschatus*	*stigmatus* Koteja	Ba	Koteja, 2008	Macropterous male
		vysniauskasi Koteja	Ba	Idem	Macropterous male
	†*Pseudoweitschatus*	***audebertis* Vea and Grimaldi**	Bu	Herein	Macropterous male
Xylococcidae	†*Baisococcus*	*victoriae* Koteja	Si	Koteja, 1989a; Koteja, 2000a for classification	Macropterous male
	Xylococcus	*grabenhorstii* Koteja	Bi	Koteja, 2008	Macropterous male
		kutscheri Koteja	Bi	Idem	Macropterous male

Family	Genus	Species	Deposit	Reference(s)	Life stage
Incertae sedis	**†*Alacrena***	***peculiaris* Vea and Grimaldi**	Bu	Herein	Macropterous male
	†*Magnilens*	***glaesaria* Vea and Grimaldi**	Bu	Herein	Macropterous male
	†*Marmyan*	*barbarae* Koteja	Bu	Koteja, 2004	Macropterous male
	†*Pedicellicoccus*	***marginatus* Vea and Grimaldi**	Bu	Herein	Macropterous male
	†*Xiphos*	***vani* Vea and Grimaldi**	Le	Herein	Macropterous male

their appendages and are hidden under secreted hard covers, explaining the elongated spinelike penial sheath of males to access the female for mating. This family is also probably recently diversified and *Normarkicoccus* could possibly suggest that early female Diaspididae may have not evolved a hard cover yet. Fossils of Diaspididae are also 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, Silesian University, 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* Koteja, 2004), from the Burmese amber collection in the Natural History Museum, London. Additionally, Vea and Grimaldi (2012) described two new species in the genus *Burmorthezia* (Ortheziidae) based on late instar nymphs, from Burmese amber. Thus, a total of 12 species and 11 genera in six 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, *Rosahendersonia prisca,* n. sp. Despite the unique combination of characters that defines it as a new genus, *Rosahendersonia* 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), *Alacrena,* n. gen., *Magnilens,* n. gen., and *Pedicellicoccus,* n. gen. In general, most of the Coccoidea taxa in Burmese amber are morphologically diverse and quite different from the Recent fauna. More particularly, the genera described as incertae sedis are similar to taxa that are scarce today,

TABLE 2. Comparative table of key characters among xylococcid-like taxa.

	Recent Xylococcidae (From Hodgson and Foldi, 2006)	*Xylococcus* (from Koteja, 2008)	*Arnoldus* (from Koteja, 2008)	*Grohnus* (from Koteja, 2008)	*Serafinus* (from Koteja, 2008)	*Weitschatus* (from Koteja, 2008)	*Xiphos*, n. gen.	*Pseudoweitschatus* n. gen.
Antennal capitate setae	absent	absent	present	absent	absent	absent	absent	absent
Pterostigma on forewing	absent	absent	absent	absent	absent	present	absent	present
Radial sector on wing	?	present	absent	absent	absent	absent	absent	absent
Hamulohaltere	leaf shape	leaf shape	leaf shape	leaf shape	leaf shape	bilobed	?	leaf shape
Basisternal median ridge	present/ light	?	?	?	absent	absent/ present	partial	?
# clusters of tubular ducts	2	2	2	2	2	2	2	2
Small caudal extension on tergite VIII	absent	absent	present	present	absent	present	absent	absent
Tarsal digitule	undifferentiated	undifferentiated	clavate	undifferentiated	undifferentiated	undifferentiated	clavate	undifferentiated
Penial sheath	short	short	short	short	short	short	elongate	short
Anterior margin of scutellum	round	round	round	pointed	round	round	pointed	?
Membranous lateral areas of scutellum	no	no	no	yes	no	no	yes	no

namely Putoidae, Phenacoleachiidae, Steingeliidae and Pityococcidae. All four families account for less than 70 species among the some 8,000 Coccoidea species. This reflects the poor knowledge within these taxa, but also the much higher diversity in the fossil shows a multitude of related extinct groups that are not representative of today's diversity.

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. Among them, two problematic genera were described, *Pennygullania* and *Palaeotupo*, respectively classified in Pennygullaniidae and Putoidae. Pennygullaniidae was later considered as a subjective synonym of Pseudococcidae by Gavrilov–Zimin and Danzig (2012) based on the lack of positive apomorphies of *Pennygullania* with Pseudococcidae. After examination of the original material by the first author, *Pennygullania electrina* needs redescriptive work as some characters have been omitted in the original description and illustration. Our phylogenetic results does not retrieve *Pennygullania* related to any of the sampled Pseudococcidae and is therefore still considered to be in Pennygullaniidae. *Palaeotupo* has been described as a putative fossil Putoidae from Cretaceous Lebanese amber, but our analysis failed to retrieve it as closely related to Putoidae. Additionally, based on the presence of more than one row of eyes (Koteja and Azar, 2008), the assignment to Putoidae remains doubtful. Our study adds four new species from the Lebanese 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.

The most significant discovery concerns two specimens here considered to be the earliest "mealybugs" (probably Phenacoccinae, Pseudococcidae), related 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 *Williamsicoccus,* n. gen., in Lebanese amber, and *Gilderius,* n. gen., in Burmese amber, as well as the putative coccid *Rosahendersonia,* 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, resulting in the descriptions of new families and genera incertae familiae.

Although most of these taxa have been described within archaeococcoid 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 archaeococcoid families have been inter alia characterized by a significantly larger body size than that of neococcoids. There is only one significantly large archaeococcoid 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 archaeococcoids. Many of the coccoids in Lebanese and Burmese ambers not only have an elongate penial sheath, some are definitively assigned to archaeococcoid groups (e.g., *Albicoccus, Burmacoccus, Kozarius*, *Xiphos*). There is no direct evidence or functional/adaptive explanation as to why an elongate penial sheath occurs in many Cretaceous taxa.

Attempting to assess the relationships of newly described fossil taxa relative to Recent taxa is becoming a critical part of studies in systematics and can substantially impact divergence time analyses prior assumptions (e.g., Ware et al., 2010). Formal phylogenetic frameworks are essential and need the use of comparative morphology alongside molecular data. However, establishing homologies between freshly collected material and fossils in different types of preservation can be challenging. The study of inclusions in amber offers a unique opportunity to access external morphology with almost no deformation, as seen in rock impressions and compressions. In this study, incorporating fossil coccoids still presents several challenges, such as the virtual absence of female scale insects in the fossil record, mirrored by the scarce knowledge of Recent males. Furthermore, the accentuated sexual dimorphism characteristic of the superfamily does not always allow an assertive association of both sexes. The main challenge, however, remains in accessing microscopic characters such as secretion pores, substantially used in recent coccoid systematics. Nondestructive methods such as high-resolution synchrotron tomography could help reveal these types of characters (Perreau and Tafforeau, 2011). Alternatively, traditional study methods of coccoids involves slide-mount preparations, but in the case of macropterous males, deformation and loss of wing venation (Koteja, 2008; Simon, 2013) can engender some bias. Thus, we advise that alternative methods preserving the general shape of specimens be more frequently used, such as scanning electron microscopy or confocal laser scanning microscopy to more easily compare fossil and Recent 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 in relation with the phylogenetic interpretation of the fossil taxa, which will require, at the very least, an expansion of knowledge and rigorous analysis of male morphology (but see Hodgson and Hardy, 2013).

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APPENDIX

Taxa Sampled for Morphological Coding and Phylogenetic Analysis

Abbreviations: **AMNH,** American Museum of Natural History; **MCZ,** Museum of Comparative Zoology, Harvard University; **MNHN,** Muséum National d'Histoire Naturelle; **NHM,** Natural History Museum, London; **USNM,** US National Museum (the scale insect collection is housed at the USDA laboratories, Beltsville, MD). Percentages of coded characters were calculated from a Nexus format file obtained from Mesquite, with a script written in Python, available in the first author's Github depository (https://github.com/zourloubidou/morphomatrix_missingdata).

	Family	Species	Recent/ fossil deposit	Coding source (collection name when specimen examined)	Coded ♂ chars. (%)	Coded ♀ chars. (%)
1	Aclerdidae	*Aclerda arundinariae* McConnell	Recent	USNM, Nada et al. (1976)	98.39	100
2	Adelgidae	*Adelges tsugae* Annand	Recent	USNM	89.52	20
3	Adelgidae	*Pineus strobi* (Hartig)	Recent	USNM	90.32	100
4	Albicoccidae	*Albicoccus dimai* Koteja	Burmese	Koteja (2004)	50	0
5	Aphididae	*Acyrthosiphon pisum* Harris	Recent	USNM	96.77	94
6	Aphididae	*Eucallipterus tiliae* (L.)	Recent	Hodgson and Foldi (2006)	96.77	6
7	Aphididae	*Ropalosiphum padi* (L.)	Recent	USNM	64.52	100
8	Apticoccidae	*Apticoccus fortis* Vea and Grimaldi (herein)	Lebanese	MNHN, Koteja and Azar (2008)	63.71	0
9	Apticoccidae	*Apticoccus longitenuis* Vea and Grimaldi (herein)	Lebanese	MNHN, Koteja and Azar (2008)	61.29	0
10	Apticoccidae	*Apticoccus minutus* Koteja and Azar	Lebanese	MNHN, Koteja and Azar (2008)	64.52	0
11	Arnoldidae	*Arnoldus capitatus* Koteja	Baltic	Koteja (2008)	61.29	0
12	Beesoniidae	*Beesonia dipterocarpi* Green	Recent	Green (1926)	90.32	100
13	Beesoniidae	*Gallacoccus secundus* Beardsley	Recent	USNM, Tagaki (2001)	88.71	100
14	Burmacoccidae	*Burmacoccus danyi* Koteja	Burmese	Koteja (2004)	54.84	0
15	Callipappidae	*Callipappus sp.*	Recent	Hodgson and Foldi (2006)	100	96
15	Cerococcidae	*Cerococcus artemisiae* (Cockerell)	Recent	USNM	94.35	94
17	Coccidae	*Ceroplastes japonicus* Green	Recent	Rainato and Pellizzari (2008), USNM	100	98

	Family	Species	Recent/ fossil deposit	Coding source (collection name when specimen examined)	Coded ♂ chars. (%)	Coded ♀ chars. (%)
18	Coccidae	*Coccus hesperidum* L.	Recent	Giliomee (1967), USNM	99.19	100
19	Coccidae	*Eulecanium tiliae* (L.)	Recent	Giliomee (1967), USNM	100	96
20	Coccidae	*Rosahendersonia prisca* Vea and Grimaldi (herein)	Burmese	AMNH	62.90	0
21	Coelostomidiidae	*Coelostomidia pilosa* (Maskell)	Recent	Hodgson and Foldi (2006), USNM	99.19	98
22	Coelostomidiidae	*Coelostomidia wairoensis* (Maskell)	Recent	Hodgson and Foldi (2006), USNM	99.19	100
23	Coelostomidiidae	*Ultracoelostomidia assimile* (Maskell)	Recent	USNM, Hodgson and Foldi (2006), Morrison (1928)	98.39	98
24	Conchaspididae	*Conchaspis lata* Hempel	Recent	USNM	98.39	100
25	Dactylopiidae	*Dactylopius coccus* Costa	Recent	Pérez Guerra and Kosztarab (1992)	100	100
26	Dactylopiidae	*Dactylopius confusus* (Cockerell)	Recent	Unpublished drawing (Hodgson pers. com), USNM	99.19	100
27	Diaspididae	*Aonidiella aurantii* (Maskell)	Recent	Ghauri (1962), USNM	100	100
28	Diaspididae	*Chionaspis salicis* (L.)	Recent	Ghauri (1962), USNM	100	100
29	Diaspididae	*Normarkicoccus cambayae* Vea and Grimaldi (herein)	Cambay	BSIP	54.03	0
30	Diaspididae	*Parlatoria oleae* (Colvée)	Recent	Ghauri (1962), USNM	99.19	100
31	Electrococcidae	*Electrococcus canadensis* Beardsley	Canada	MCZ, Beardsley (1969)	68.55	0
32	Eriococcidae	*Eriococcus buxi* (Boyer de Fonscolombe)	Recent	USNM	100	98
33	Eriococcidae	*Eriococcus coccineus* Cockerell	Recent	USNM	100	100
34	Eriococcidae	*Kuenowicoccus pietrzeniukae* Koteja	Baltic	Koteja (1988b)	66.94	0
35	Eriococcidae	*Ovaticoccus agavium* (Douglas)	Recent	USNM	100	100
36	Eriococcidae	*Tanyscelis verrucula* (Froggatt)	Recent	USNM	87.9	98
37	Grimaldiellidae	*Grimaldiella gregaria* Koteja	New Jersey	AMNH, Koteja (2000b)	79.84	0
38	Grohniidae	*Grohnus eichmanni* Koteja	Baltic	Koteja (2008)	66.94	0
39	Hodgsonicoccidae	*Hodgsonicoccus patefactus* Vea and Grimaldi (herein)	Lebanese	AMNH, Koteja and Azar (2008)	71.77	0
40	Incertae sedis	*Alacrena peculiaris* Vea and Grimaldi (herein)	Burmese	AMNH	58.06	0
41	Incertae sedis	*Magnaelentes glaesaria* Vea and Grimaldi (herein)	Burmese	AMNH	58.06	0
42	Incertae sedis	*Marmyan barbarae* Koteja	Burmese	Koteja (2004)	41.94	0
43	Incertae sedis	*Pedicellococcus marginatus* Vea and Grimaldi (herein)	Burmese	AMNH	61.29	0
44	Incertae sedis	*Xiphos vani* Vea and Grimaldi (herein)	Lebanese	MNHN	72.58	0
45	Incertae sedis	Undescribed specimen ARC 60.1	French	Université de Rennes 1, Géosciences	39.52	0
46	Inkaidae	*Inka minuta* Koteja	Taymir	Koteja (2000b)	80.65	0
47	Jersicoccidae	*Jersicoccus kurthi* Koteja	New Jersey	AMNH, Koteja (2000b)	43.55	0
48	Kermesidae	*Kermes quercus* (L.)	Recent	USNM	96.77	98
49	Kermesidae	*Kermes* sp.	Recent	USNM	94.35	0
50	Kerriidae	*Tachardina aurantiaca* (Cockerell)	Recent	USNM, unpublished drawing (Hodgson pers. com)	100	100
51	Kozariidae	*Kozarius achronus* Vea and Grimaldi (herein)	Burmese	AMNH	76.61	0
52	Kozariidae	*Kozarius perpetuus* Vea and Grimaldi (herein)	Burmese	AMNH	77.42	0
53	Kukaspididae	*Kukaspis usingeri* Koteja and Poinar	Alaska	Koteja and Poinar (2001)	66.13	0

	Family	Species	Recent/ fossil deposit	Coding source (collection name when specimen examined)	Coded ♂ chars. (%)	Coded ♀ chars. (%)
54	Kuwaniidae	*Neosteingelia texana* Morrison	Recent	USNM, Hodgson and Foldi (2006), Morrison (1928)	100	100
55	Labiococcidae	*Solicoccus nascimbene* Koteja	New Jersey	AMNH, Koteja (2000b)	66.13	0
56	Lebanococcidae	*Lebanococcus longiventris* Koteja and Azar	Lebanese	MNHN, Koteja and Azar (2008)	62.90	0
57	Lecanodiaspididae	*Lecanodiaspis baculifera* Leonardi	Recent	USNM	91.13	100
58	Margarodidae	*Dimargarodes meridionalis* (Morrison)	Recent	USNM	97.58	98
59	Margarodidae	*Dimargarodes tanganyi* Jakubski	Recent	Hodgson and Foldi (2006), USNM	98.39	98
60	Margarodidae	*Heteromargarodes americanus* (Jakubski)	Recent	USNM, Hodgson and Foldi (2006)	100	98
61	Margarodidae	*Heteromargarodes hukamsinghi* Vea and Grimaldi (herein)	Cambay	BSIP	58.87	0
62	Margarodidae	*Porphyrophora hamelii* Brandt in Brandt and Ratzeburg	Recent	USNM, Hodgson and Foldi (2006)	100	100
63	Matsucoccidae	*Eomatsucoccus casei* Koteja	New Jersey	AMNH, Koteja (2000b)	51.61	0
64	Matsucoccidae	*Matsucoccus bisetosus* Morrison	Recent	USNM	81.45	100
65	Matsucoccidae	*Matsucoccus feytaudi* Ducasse	Recent	USNM	97.58	100
66	Matsucoccidae	*Matsucoccus josephi* Bodenheimer and Harpaz in Bodenheimer and Neumark	Recent	USNM	100	100
67	Matsucoccidae	*Matsucoccus matsumurae* Kuwana	Recent	USNM	95.97	100
68	Monophlebidae	*Drosicha corpulenta* (Kuwana)	Recent	USNM, Hodgson and Foldi (2006)	98.39	100
69	Monophlebidae	*Drosicha dalbergiae* (Stebbing)	Recent	Hodgson and Foldi (2006)	99.19	100
70	Monophlebidae	*Drosicha pinicola* (Kuwana)	Recent	USNM, Hodgson and Foldi (2006)	98.39	100
71	Monophlebidae	*Gigantococcus maximus* (Newstead)	Recent	USNM, Hodgson and Foldi (2006)	98.39	100
72	Monophlebidae	*Icerya purchasi* Maskell	Recent	USNM, Hodgson and Foldi (2006)	100	98
73	Monophlebidae	*Icerya seychellarum* (Westwood)	Recent	USNM, Morrison (1928)	100	100
74	Monophlebidae	*Palaeococcus fuscipennis* (Burmeister)	Recent	USNM, Hodgson and Foldi (2006), Vayssière (1926)	97.58	98
75	Ortheziidae	*Cretorthezia hammanaica* Koteja	Lebanese	MNHN, Koteja and Azar (2008)	50	0
76	Ortheziidae	*Insignorthezia insignis* (Browne)	Recent	USNM, Kozár (2004)	96.77	100
77	Ortheziidae	*Newsteadia floccosa* (De Geer)	Recent	USNM, Kozár (2004), Koteja (1986a),	99.19	100
78	Ortheziidae	*Orthezia urticae* (L.)	Recent	Koteja (1986), USNM, Kozár (2004)	99.19	100
79	Ortheziidae	*Palaeonewsteadia huanae* Koteja	Baltic	Koteja (1987a)	72.58	0
80	Ortheziidae	*Praelongorthezia praelonga* (Douglas)	Recent	NHM, USNM, Kozár (2004)	96.77	98
81	Ortheziidae	*Protorthezia aurea* Koteja	Baltic	Koteja (1987b)	62.90	0
82	Pennygullaniidae	*Pennygullania electrina* Koteja and Azar	Lebanese	MNHN, Koteja and Azar (2008)	60.48	0
83	Phenacoleachiidae	*Phenacoleachia species* a in Hodgson and Foldi, 2006	Recent	Hodgson and Foldi (2006)	99.19	100
84	Phenacoleachiidae	*Phenacoleachia species* b in Hodgson and Foldi, 2006	Recent	Hodgson and Foldi (2006)	97.58	0

	Family	Species	Recent/ fossil deposit	Coding source (collection name when specimen examined)	Coded ♂ chars. (%)	Coded ♀ chars. (%)
85	Pityococcidae	*Pityococcus moniliformalis* Vea and Grimaldi (herein)	Baltic	AMNH	90.32	0
86	Pityococcidae	*Pityococcus* sp. in Hodgson and Foldi, 2006	Recent	Hodgson and Foldi (2006)	99.19	100
87	Pseudococcidae	*Antonina graminis* (Maskell) (female) *A.crawii* Cockerell (male)	Recent	USNM	99.19	100
88	Pseudococcidae	*Ceroputo pilosellae* (Sulc)	Recent	USNM, Afifi (1968)	98.39	96
89	Pseudococcidae	*Coccidohystrix insolita* (Green)	Recent	USNM	96.77	100
90	Pseudococcidae	*Dysmicoccus grassii* (Leonardi)	Recent	USNM, Afifi (1968)	98.39	100
91	Pseudococcidae	*Ferrisia virgata* (Cockerell)	Recent	USNM, Afifi (1968)	99.19	98
92	Pseudococcidae	*Gilderius eukrinops* Vea and Grimaldi (herein)	Burmese	AMNH	65.32	0
93	Pseudococcidae	*Planococcus citri* (Risso)	Recent	USNM, Afifi (1968)	100	100
94	Pseudococcidae	*Pseudococcus longispinus* (Targioni Tozzetti)	Recent	USNM, Afifi (1968)	98.39	100
95	Pseudococcidae	*Pseudococcus maritimus* (Ehrhorn)	Recent	USNM, Afifi (1968)	76.61	100
96	Pseudococcidae	*Williamsicoccus megalops* Vea and Grimaldi (herein)	Lebanese	MNHN, Koteja and Azar (2008)	61.29	0
97	Putoidae	*Palaeotupo danielae* Koteja and Azar	Lebanese	MNHN, Koteja and Azar (2008)	63.71	0
98	Putoidae	*Puto kozstarabi* Miller and Miller	Recent	USNM	98.39	100
99	Putoidae	*Puto mexicanus* (Cockerell)	Recent	USNM	95.97	100
100	Putoidae	*Puto yuccae* (Coquillett)	Recent	USNM, Hodgson and Foldi (2006)	100	100
101	Serafinidae	*Serafinus acupiterus* Koteja	Baltic	Koteja (2008)	80.65	0
102	Steingeliidae	*Palaeosteingelia acrai* Koteja and Azar	Lebanese	MNHN, Koteja and Azar (2008)	76.61	0
103	Steingeliidae	*Steingelia gorodetskia* Nasonov	Recent	USNM, Hodgson and Foldi (2006), Morrison (1928)	99.19	100
104	Steingeliidae	*Steingelia cretacea* Koteja	New Jersey	AMNH, Koteja (2000b)	73.39	0
105	Stictococcidae	*Strictococcus vayssievei* Richard	Recent	USNM, unpublished drawing (Hodgson, personal commun.)	88.71	98
106	Stigmacoccidae	*Stigmacoccus asper* Hempel	Recent	USNM, Hodgson and Foldi (2006)	99.19	98
107	Electrococcidae	*Turonicoccus beardleyi* Koteja	New Jersey	AMNH, Koteja (2000b)	45.16	0
108	Weitschatidae	*Pseudoweitschatus audebertis* Vea and Grimaldi (herein)	Burmese	AMNH	73.39	0
109	Weitschatidae	*Weitschatus stigmatus* Koteja	Baltic	Koteja (2008)	91.13	0
110	Xylococcidae	*Xylococculus betulae* (Pergande in Hubbard and Pergande)	Recent	Hodgson and Foldi (2006), Morrison (1928)	99.19	100
111	Xylococcidae	*Xylococcus grabenhorsti* Koteja	Baltic	Koteja (2008)	74.19	0
112	Xylococcidae	*Xylococcus japonicus* Oguma	Recent	Hodgson and Foldi (2006)	99.19	98