

## Scale insects from Lower Cretaceous amber of Lebanon (Hemiptera: Sternorrhyncha: Coccinea)

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### ABSTRACT

Results of investigations on Lower Cretaceous Lebanese amber (125 - 135 myr) are presented, based on amber pieces containing coccid inclusions, collected in Mdeyrij/Hammana in central Lebanon and (one inclusion) in Jezzine in southern Lebanon. Seven groups at family level have been recognized, one extant, two supposedly extant, one extinct and three new families: Ortheziidae with *Cretorthezia hammanaica* gen. et sp. n.; Hammanococcidae fam. n. with *Hammanococcus setosus* gen. et sp. n.; Lebanococcidae fam. n. with *Lebanococcus longiventris* gen. et sp. n.; ?Steingeliidae with *Palaeosteingelia* gen. n. and *P. acrai* sp. n. and *P. caudata* sp. n.; ?Electrococcidae with *Apticoccus minutus* gen. et sp. n.; ?Putoidae with *Palaeotupo danieleae* gen. et sp. n.; and Pennygullaniidae fam. n. with *Pennygullania electrina* gen. et sp. n. All taxa have been based on alate males; two crawlers and two older stage larvae are believed to be congeneric with *Cretorthezia*, *Hammanococcus*, *Palaeosteingelia* and *Pennygullania*.

All species bear peculiar features or combinations of characteristics, but there is no doubt as to their coccid affiliation. Archeococcid groups predominate in the Lebanese amber fauna, compared with neococcids which are represented by a form related to Putoidae and a species that cannot be placed in any extant group. Considering also impression fossils, the Lower Cretaceous fauna is represented by seven archeococcid and two neococcid families. Coccids similar to extant Steingeliidae constitute about 55 % of the Lebanese scale insects (18 inclusions); other groups are represented by 1-3 inclusions. Similar proportions have been found in New Jersey amber (with Grimaldiellidae dominating), Taimyr amber (Inkaidae dominating), and Baltic amber (Matsucoccidae prevailing). It is suggested that all or most of the species found in Lebanese amber fed on the resin exudating host, supposedly an araucarian, or a cheirolepidian.

**KEY WORDS:** Scale insects. Coccinea. Amber. Lower Cretaceous. Lebanon

### INTRODUCTION

The Lebanese amber belongs to the Middle-East Lower Cretaceous fossil resins that occur in Lebanon, Jordan, Syria and Israel. First mentioned in Lebanon by Joseph von Russeger in 1843 in coal mines near Beirut then by Oscar Frass in 1878 in southern Lebanon and by Godefroy Zumoffen in several localities in 1926, the amber was then intensively studied by several workers (for review see Poinar 1992, Borkent 2000). For the present the most important field explorations have been carried out by Professor Aftim Acra and his son Fadi in the 60-70tees and later by one of us D. Azar (Azar & Nel 1998, Azar 2000) and his team who discovered more than 275 outcrops.

The Lebanese amber is a valuable source of information on Lower Cretaceous insects, especially of small-sized groups. The occurrence of scale insects in Lebanese amber was first mentioned by Schlee & Dietrich (1970); there also is scattered information on the existence of coccids in various collections but none was available for study or described until now.

The Lebanese coccids are not the only known from the Cretaceous times. The first Cretaceous coccid was described by Beardsley (1969) from Canadian amber, further fossils were described from Upper Cretaceous Taimyrian, New Jersey, Myanmar and Alaskan amber and from Lower Cretaceous rocky impressions (Koteja 1999b, 2000a, 2004). In the latter paper also the concept of the scale insect paleontology was broadly discussed.

The present study is based on several amber inclusions which constitute, together with the few impressions, the oldest evidence of the scale insect history.

### MATERIAL

The material studied herein comes from two regions of Lebanon: Mdeyrij/Hammana, central Lebanon and Jouar Ess-Souss (known in literature as Jezzine outcrop), southern Lebanon, both Lower Cretaceous in age, ca 125 - 135 million years old, and assumed to be produced by araucarians (Poinar & Milki 2001), or cheirolepidian (Dejax, pers. comm.). Most of the amber pieces were a few

COCC-	depository	taxon	instar
0845	HAM -36	<i>Palaeosteingelia</i> sp.	mi
0846	HAM -44	<i>Palaeosteingelia acraei</i>	mi
0847	HAM -54	<i>Apticoccus minutus</i>	mi
0848	HAM -86	<i>Palaeosteingelia</i> sp.	lc
0849	HAM -381	<i>Pennygullania electrina</i>	mi
0850	HAM -408	<i>Hammanococcus</i> sp.	mi
0851	HAM -409	<i>Palaeosteingelia acraei</i>	mi
0852	HAM -410	<i>Palaeosteingelia acraei</i>	mi
0853	HAM -411	<i>Palaeosteingelia acraei</i>	mi
0854	HAM -412	<i>Palaeosteingelia acraei</i>	mi
855a-c	HAM -413A-C	<i>Palaeosteingelia acraei</i>	mi
0856	HAM -414	<i>Palaeosteingelia acraei</i>	mi
0857	HAM -415A	<i>Palaeosteingelia acraei</i>	mi
0858	HAM -416	<i>Palaeosteingelia caudata</i>	mi
0859	HAM -417	<i>Palaeosteingelia acraei</i>	mi
860ab	HAM -418	<i>Palaeosteingelia caudata</i>	mi
1315	HAM -140C	<i>Lebanococcus longiventris</i>	mi
1316	HAM -436E	<i>Cretorthezia hammanaica</i>	mi
1317ab	HAM -555B,D	<i>Palaeosteingelia</i> sp.	mi
1317c	HAM -555E	<i>Hammanococcus setosus</i>	mi
1318	HAM -580	<i>Palaeosteingelia acraei</i>	mi
1319	HAM -581	<i>Palaeosteingelia acraei</i>	mi
1320	HAM -582	<i>Palaeotupo danieleae</i>	mi
1321	HAM -583	<i>Pennygullania</i> sp.	lc
1322	HAM -584	<i>Palaeosteingelia acraei</i>	mi
1323	HAM -585	<i>Palaeosteingelia acraei</i>	mi
1324	JS-95, BM-53	<i>Cretorthezia</i> sp.	la
1354	HAM -475	<i>Hammanococcus</i> sp.	la
1579	HAM -592A	<i>Palaeosteingelia acraei</i>	mi

Abbreviations: mi = male imago, lc = crawler, la = older stage larva, st-h = stellate hairs, frag. = fragments.

Table 1. Lebanese amber inclusions available for the present study.

millimeters in size after preparation. The amber is brittle and soft. In general appearance and handling it reminds Alaskan, Canadian and some pieces of New Jersey amber.

34 coccid amber inclusions were available for this study; some pieces contained more than one inclusion and in one instance representatives of different groups were present (see table 1).

Almost all inclusions were originally completely impregnated with resin; *i.e.*, the light breaking surface between inclusion and resin, so characteristic of Baltic amber inclusions, is lacking in the Lebanese amber, and the body, with the translucent muscles and other tissues, assume a brown, sometimes a very dark, colour, and many parts, especially the abdomen and antennae become shrivelled. On the other hand, "milky clouds" round inclusions, very common in Baltic amber, are rare in Lebanese amber. Very rarely, some body parts (*e.g.*, the legs) are swollen as a result putrefaction of tissues.

The material dealt with in the present study was collected by the junior author in central Lebanon (1996-99) and one piece (JS-95, BM-53) or (Cocc-1324) collected by Prof. Aftim Acra and his son Fadi in southern Lebanon (1967-70). Material is temporarily housed in at the Muséum National d'Histoire Naturelle, Paris, in waiting the creation of a national natural history museum in Lebanon.

## METHODS

All amber pieces have been prepared, *i. e.*, dissected, ground, polished and embedded in Canada balsam between slide and cover slips or two cover slips as proposed by Azar (2000) and Azar et al. (2003).

Each amber piece is provided with its real number of the specimens and is indicated by the initials "HAM-", *e.g.*, HAM-555E. "HAM-" for Hammana amber deposit, followed by the specimen number, then when the specimen contains or contained originally more than one inclusion, upper case letter(s) is (are) annexed indicating as so the number of the inclusion within the specimen.

The specimen from the Acra collection, bears additional label numbers JS-95 and BM-53, the former "J" referring to Jezzine and "S" to single indicating that the amber piece has not been broken during excavation or preparation, the latter "BM" referring to the Natural History Museum of London in which it was examined.

The second label number (between brackets) refers to a consecutive number of the virtual "coccid fossils world collection" preceded with "Cocc-"; inclusions, if more than one in a piece, receive lower case letters "a", "b" etc.; for instance, Cocc-1317a-c indicates that 3 coccids were embedded in this piece, independent of whether of the same or different species. These numbers are added to each dissected piece to make possible identification of the described specimens. This procedure has been adopted because many inclusions in both private and public collections do not bear inventory numbers (Koteja 1984, 2000b).

An Olympus SZH stereoscope and Zeiss NfpK microscope (objectives from 4x to 40x) equipped by a camera lucida and changeable direct and transmitted light were used for microscopic examination. Antennae, legs and wings may be deformed and optically shortened in total figures. Antennal joints and abdominal segments are flattened, thus appearing broader than they actually are. Measurements, especially of entire body, are approximate only because of shrivelling and various optical deformations.

The description of males and morphological nomenclature has been adopted from Theron (1958) and Koteja (1986), and that referring to wings from Morrison (1928) and Koteja (1996). The length of tarsus was measured including claw, unless otherwise stated. The name "coccids" refers to scale insects (Coccoinea) throughout the text; "archeococcids" to the superfamily Orthezioidea; "neococcids" to the superfamily Coccoidea.

**SYSTEMATIC PALAEOONTOLOGY**

Seven taxa at family level have been recognized among the Lebanese inclusions, including 3 extant and 4 extinct families:

Order: Hemiptera Linnaeus 1758

Suborder: Sternorrhyncha Duméril 1806

Infraorder: Coccinea Fallén 1814

Superfamily: Orthezioidea Orthezioidea Amyot & Serville 1843

1. Ortheziidae Amyot & Serville 1843 with *Cretorthezia hammanaica* gen. et sp. nov.

2. Hammanococcidae fam. n., with *Hammanococcus setosus* gen. et sp. nov.

3. Lebanococcidae fam. n., with *Lebanococcus longiventris* gen. et sp. nov.

4. Steingeliidae Morrison 1927 with *Palaeosteingelia* gen. nov.,

and *P. acraei* sp. n. and *P. caudata* sp. nov.

5. Electrococcidae Koteja 2000 with *Apticoccus minutus* gen. et sp. nov.

Superfamily: Coccoidea Fallén, 1814

6. Putoideae Beardsley 1969 with *Palaeotupo danieleeae* gen. et sp. nov.

7. Pennygullaniidae fam. n., with *Pennygullania electrina* gen. et sp. nov.

Key to the Lebanese amber inclusions

1. Alate forms (males).....2

- . Apterous forms (larvae and/or females) .....8

2. With compound eyes .....3

- . With simple eyes .....5

3. Scutellum oval, appendages very long and slender...  
*Cretorthezia hammanaica*

- . Scutellum triangular, appendages of moderate length or short .....4

4. Abdomen evenly tapering, of telescopic structure, appendages very short, with capitate setae on antenna and tarsus .....*Lebanococcus longiventris*

- . Abdomen cylindrical, with very long setae on margins of 6th abdominal segment, antenna and tarsus without capitate setae .....*Hammanococcus setosus*

5. With a pair of dorsal and a pair of ventral simple eyes; two posterior abdominal segments with strong caudal setae.....*Pennygullania electrina*

- . With a row of 6-7 simple eyes on each side of head, strong caudal setae on last abdominal segment or tail setae absent .....6

6. Wing broad (wider than half its length) without microtrichia with two or more pairs of waxy tail filaments  
*Palaeosteingelia* (two species)

- . Wing narrow (width smaller than half its length) with microtrichia, with one pair of waxy tails or tail devices lacking.....7

7. Medium sized, with a pair of glandular pouches on last abdominal segment, each associated with two strong setae, scutellum triangular with one angle directed rearward, with double row of simple eyes .....*Palaeotupo danieleeae*

- . Minute, with 4 short caudal setae (no wax glands), scutellum tubular, simple eyes forming one row .....  
*Apticoccus minutus*

8. With conspicuous wax plates on body margin .....  
*?Cretorthezia*

- . Without such waxy plates .....9

9. With protruding anal lobes and setigerous anal ring .  
*?Pennygullania*

- . Without protruding anal lobes and setigerous anal ring .....10

10. With a pair of small caudal setae (ca 35 µm) .....  
*?Palaeosteingelia*

- . With a pair of conspicuous caudal setae (ca 350 µm) and numerous other setae.....

*?Hammanococcus*

Order: Hemiptera Linnaeus 1758

Suborder: Sternorrhyncha Duméril 1806

Infraorder: Coccinea Fallén 1814

Superfamily: Orthezioidea Amyot & Serville 1843

Family: Ortheziidae Amyot & Serville 1843

GENUS: *Cretorthezia* gen. nov.

Type species: *Cretorthezia hammanaica* sp. nov., alate male

**Etymology.** The generic name refers to Cretaceous time in which the inclusion bearing amber originated. Grammatical gender: feminine.

**Diagnosis.** Minute ortheziid with 10-segmented antennae, two very long and one small antennal bristles on apical segment; mesosternum without medial ridge; wings spoon-like, narrow subcostal ridge, anterior flexing membrane present, cubital ridge, posterior flexing line and alar fold absent; haltere reduced; cluster of pore tubes forming tail tuft small; penial sheath conspicuous, very long, bent downward.

*Cretorthezia hammanaica* sp. nov.

(Plate 1, figures A and B)

**Etymology.** The species name refers to Hammana (Central Lebanon) in which the amber sample was collected.

**Holotype.** Alate male, specimen number HAM-436E (Cocc-1316), Azar collection, housed provisionally in the

Muséum National d'Histoire Naturelle, Paris. No other specimens available.

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Diagnosis.** As for the genus.

**Description.** Minute winged male 660  $\mu\text{m}$  long, but the abdomen is much shriveled and shortened, 180  $\mu\text{m}$  wide at

mesothorax. Head broad, 150  $\mu\text{m}$  wide, with pronouncing compound eyes, 60  $\mu\text{m}$  in diameter; ventromedial plate rhomboidal with midcranial ridge; ventral plate recognizable. Antenna long (780  $\mu\text{m}$ ), longer than body, wings and legs, slender, 10-segmented; pedicel and scape subequal, each ca 50  $\mu\text{m}$  long, with numerous short setae; flagellar joints 65-100  $\mu\text{m}$  long, first joint the longest, apical one the shortest, all slender, irregularly nodose, with numerous hair-like and fleshy setae (all acute) slightly longer than

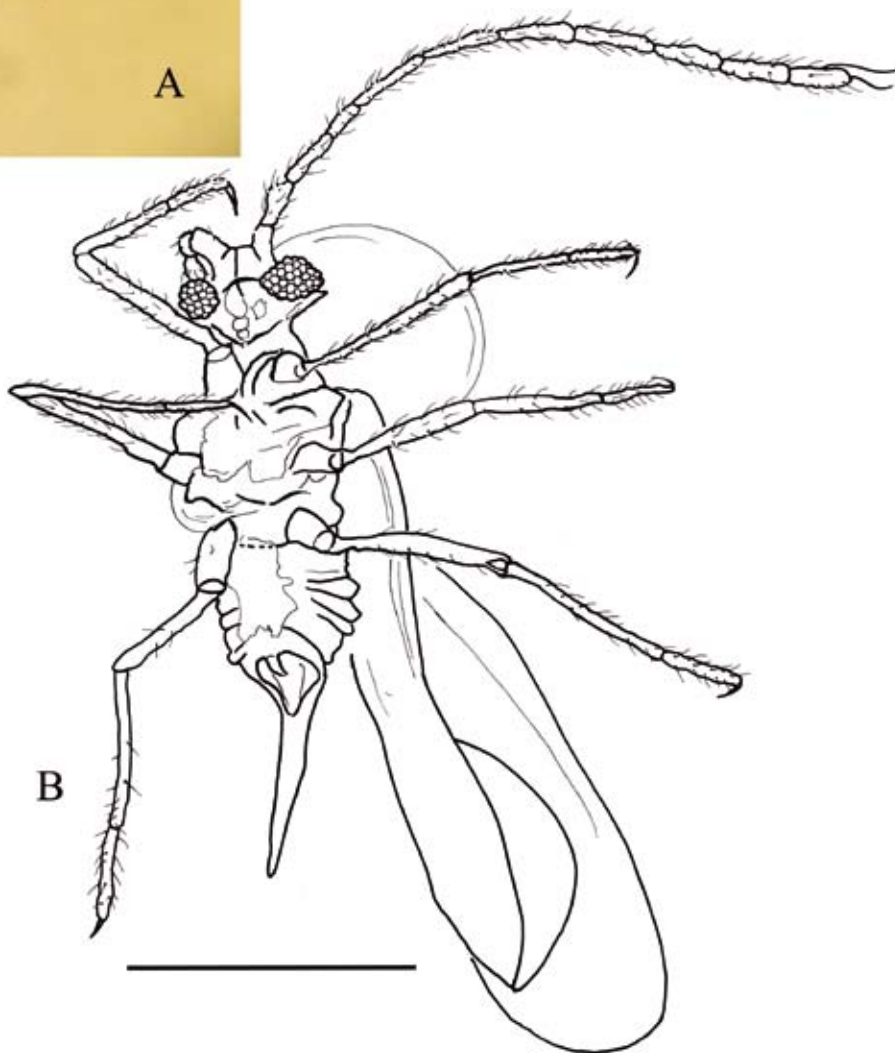


Plate 1: *Cretorthezia hammanaica* gen. et sp. n., alate male, holotype n HAM-436E (Cocc-1316). Fig. A: Photography of *Cretorthezia hammanaica* gen. et sp. n., ventral view. Fig. B: Drawing of *Cretorthezia hammanaica* gen. et sp. n., ventral view. Scale bar represents 0.3 mm.

segment width, apical segment with two conspicuous (as long as the joint), and one short, antennal bristles, fleshy and hair-like setae also present on this joint.

Prothorax shrunken, but a triangular sclerite can be recognized between forecoxae. Scutellum oval; mesosternum large, without medial ridge; metasternum large, with conspicuous furcal pit. Legs long and slender, ca 700  $\mu\text{m}$  long (forelegs perhaps the longest), trochanter and femur supposedly fused, length of joints (in  $\mu\text{m}$ ) - coxa 85, trochanter+femur 180, tibia 270, tarsus 115, claw 48; claw slender, almost straight, without digitules and denticles; all joints with inconspicuous setae, some spine-like, longer than segment width.

Wings spoon-like, narrow basally, without a fold for holding halteral setae (halteres reduced), opaque, with fine sculpture, no microtrichia, 900  $\mu\text{m}$  long, 360  $\mu\text{m}$  wide. Subcostal ridge narrow, weak, reaching 2/3 wing length, bearing about 8 cupolae (alar setae not recognized); cubital ridge apparently reduced; anterior flexing patch present, long, posterior one not recognized. Abdomen shriveled, much shortened (apparently largely membranous), with a few short setae; pore cluster small, consisting of a few (not more than 10) tubes; one wax thread preserved, attached to penial sheath. Penial sheath conspicuous, conical, of matsucoccid type, 240  $\mu\text{m}$  long, 65  $\mu\text{m}$  wide at base, slightly bent downward, with a few setae on capsule; apex of aedeagus protrudes from penial sheath.

**Note.** The Ortheziidae comprise 10 genera (2 extinct), but males have been found and described only in recent genus *Orthezia* Bosc d'Antique, 1784, *Newsteadia* Green, 1902, *Protorthesia* Koteja, 1987 and *Palaeonewsteadia* Koteja, 1987, the two latter from Baltic amber (for review see Koteja 1986, 1987a, 1987b). Ortheziid males are distinctive by the shape of head with large, forward protruding, compound eyes, very long and slender antennae and legs, and grayish colouration. The Lebanese species is an obvious ortheziid, but its relationships within the family are difficult to ascertain; in any case, it bears several derived (apomorphic) features which include: small body size, markedly reduced wing venation, entirely reduced halteres, long antennal bristles (some of the features are shared with *Newsteadia floccifera* (De Geer, 1778) and/or *Palaeonewsteadia huaniae* Koteja, 1987. Unique is the conspicuous, conical, acute penial sheath, about four times as long as wide at base (less than two times so in other genera) which also can be a derived state. Further suggestions can be proposed after males in other genera will be discovered.

#### GENUS: ?*Cretorthesia* sp., larva

(Plate 2, figures A-C)

There is a peculiar specimen with well preserved waxy cover in the Lebanese material which may be an ortheziid. However, there is no evidence now to consider it conspecific with the male *Cretorthesia hammanaica*.

**Material studied.** Older stage larva or young adult female, specimen number JS-95 BM-53 (Cocc-1324), Acra collection, housed provisionally in the Muséum National

d'Histoire Naturelle, Paris. No other specimens available. The specimen, older stage larva or adult female, is completely impregnated with resin and Canada balsam, some appendages are broken, mouthparts and anal region not visible. Wax secretions well preserved; accessible from dorsum and venter.

**Type locality and horizon.** Lower Cretaceous, Jouar Ess-Souss, Caza Jezzine, Mouhafazet Loubnan El-Janoubi (Southern Lebanon).

**Description.** Body elongate oval, almost parallel-sided, 1730  $\mu\text{m}$  long, 680  $\mu\text{m}$  wide, flattened. Antennae inserted at frontal margin ventrally, with a considerable distance between them; 6-segmented, assuming that the somewhat club shaped apical joint is one segment. Scape strong, ca 150  $\mu\text{m}$  long, with anterolateral apical articulation; pedicel, 110  $\mu\text{m}$ , similar to cylindrical flagellar segments; each of the two proximal flagellar segments 120  $\mu\text{m}$  long; penultimate joint 95  $\mu\text{m}$  long; apical joint slightly club-shaped, 280  $\mu\text{m}$  long; approximate length of antenna 875  $\mu\text{m}$ . A few hair-like setae noted on pedicel and flagellar segments, except apical one which bears numerous short setae, some spine like, but none representing characteristic ortheziid pegs (antennal bristles). Eyes much obscured, conspicuous, inserted on stalks. Mouthparts invisible. Legs strong but slender; in hindleg (other missing), coxa (ca 22  $\mu\text{m}$  long) obscured in all legs; trochanter well developed, distinctly separated from femur, both 540  $\mu\text{m}$  long, no setae noted on trochanter, a few small setae on femur; tibia 360  $\mu\text{m}$  long, with numerous short, some spine-like, setae, and strong apical spurs; tarsus 310  $\mu\text{m}$  long with numerous setae, without digitules; claw strong, 90  $\mu\text{m}$  long, slightly bent, without denticles, bearing a pair of short slender spine-like digitules at base.

Anal ring not visible; from venter hardly recognizable as a rounded structure with a few (no more than 6) short setae. Spiracles, body setae and pores not visible. Wax secretion well visible in direct light, hardly recognizable in transmitted light, of ortheziid type; consisting of about 18 pairs of lateral plates (bars), subrectangular in cross-section, longer than body width, and one or two rows of dorsal, marginal rows of smaller plates; this and the presence of median plates, cannot be ascertained; all lateral plates are slightly arched ventrad; the body with its wax covering assumes a shape of an almost circular umbrella.

**Note.** In scale insects, adult female can be recognized by the presence of vulva and egg-protecting devices; in known groups and species, also by other features (shape, size, number of antennal segments, sensilla etc.). Ortheziid egg-laying females are characteristic by the marsupium consisting of several dorsal and one ventral waxy plates. In the inclusion in question, marsupium is evidently absent, and vulva, sometimes visible in inclusions, has not been located. Other features, as size or number of antennal segments are not informative because they are diverse in the Ortheziidae (the adult antenna may consist of 3 to 8 joints in various groups). There seems to be a thin transparent plate (not shown on drawings) that may correspond with

the ortheziid ventral plate of marsupium, but this is uncertain. Concluding, the specimen may be a larva of an advanced stage or an adult female before egg deposition.

The strongest argument for affiliating the inclusion with the ortheziids is the wax covering. It consists of homogeneous secretion produced by some dermal glands (unfortu-

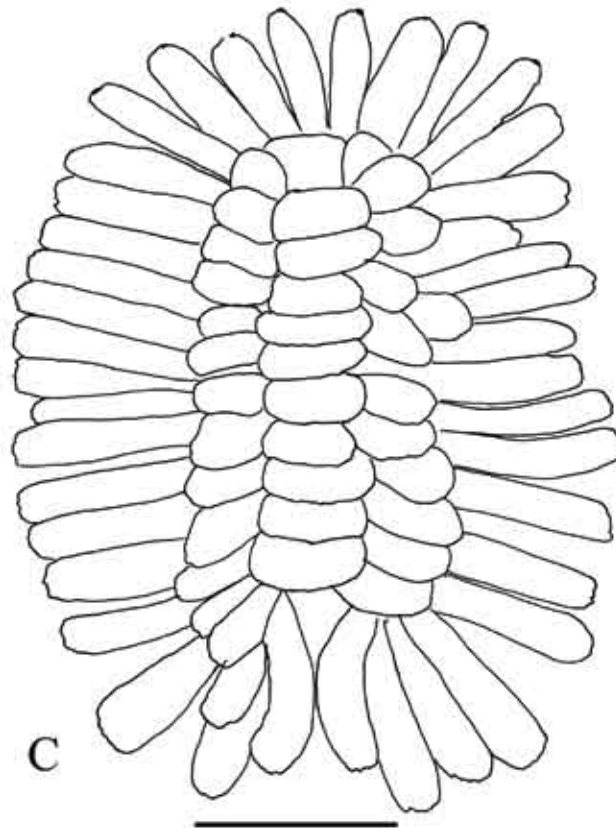


Plate 2: ?*Cretorthezia* sp. Specimen JS-95, BM-53 (Cocc-1324). Fig. A: Photography of ?*Cretorthezia* sp., dorsal view. Fig. B: Photography of ?*Cretorthezia* sp., vortal view. Fig. C: Drawing of ?*Cretorthezia* sp., dorsal view, scale bar represents 0.7 mm.

nately not recognizable) arranged in laterodorsal clusters. The number of the parallelsided, subrectangular in cross-section, plates approximates 20, but they cannot be exactly counted because, as in ortheziids, the gland clusters may be subdivided or fused. Dorsal plates apparently also occur, but their number and shape are difficult to ascertain. In other scale insects, for instance in some Pseudococcidae, the mealy wax secretions assume a conical or filamentous shape.

In all recent Ortheziidae trochanter and femur are fused. In the Lebanese specimen these joints not only are clearly separated, but the trochanter is a large slender piece, thus the objection as to its affiliation with the ortheziids. Another non-ortheziid characteristics are the setae on antennae, hair-like, uniform, very numerous on apical joint (primary conditions); in Ortheziidae, the setae are differentiated into hair- and spine like, and antennal bristles (thin-walled pegs), sometimes very long.

In general, the male must be regarded as a 'derived form', whereas the female (larval) specimen, as 'primitive', such relations do occur in other scale insects, too. No argument that the specimen in question is or not conspecific, or closely related with the male *Cretorthezia hammanaica*. Thus, for the time being, the female has been left unattached.

Family: Hammanococcidae fam. nov.

Type genus *Hammanococcus* gen. nov.

**Diagnosis.** Coelostomidiid-like archeococcids with abdomen strongly tapered; 6th segment with lateral groups of conspicuous setae dorsally and 7th segment with long sternal medial setae; penial sheath long, narrow, slightly bent.

GENUS: *Hammanococcus* gen. nov.

Type species: *Hammanococcus setosus* sp. nov., alate male

**Etymology.** The generic name refers to Hammana, region in Central Lebanon in which the inclusion bearing amber was found. Grammatical gender: masculine.

**Diagnosis.** Medium sized archeococcid, with compound eyes inserted laterally; long, 10-segmented antennae, bearing numerous conspicuous setae, but without knobbed setae on any joint; transversely oval prescutum, triangular scutellum, mesopostnotum separated from scutellum by a large membrane; mesosternum without medial ridge; legs long, tibia with a group of minute apical setae, tarsal digitules not differentiated, claw thin, without denticles, with 2 knobbed digitules longer than claw; alar lobe for holding hamuli well developed, haltere leaflike, with 2 or 3 setae; abdomen tapering, with conspicuous setae on 6th segment dorsally, and on 7th segment ventrally; penial

sheath narrow, long, slightly bent, with minute setae and a group of cupolae on apex.

*Hammanococcus setosus* sp. nov.

(Plate 3, figures A and B)

**Etymology.** Species name (Latin) refers to long setae on abdominal tergites.

**Holotype.** Alate male, specimen number HAM-555E (Cocc-1317c), Azar collection, housed provisionally in the Muséum National d'Histoire Naturelle, Paris. No other specimens available.

**Amber and inclusion.** Coccid syninclusions: two other scale insects in separate dissected pieces (c.f. *?Palaeosteingelia*, specimens' number HAM -555B, D (Cocc-1317a-b)

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Diagnosis.** As for genus.

**Description.** Medium sized (the largest in the Lebanese sample) winged male about 1500 µm long, and 300 µm wide at thorax. Head broad, 500 µm wide; compound eyes conspicuous, 180 µm in diameter, accommodated at the sides of head; ocelli on conspicuous conical projections; other structures not recognizable (almost all dorsal face of head hidden beneath prescutum). Antennae 1320 µm long, 10-segmented; pedicel 60 µm long with numerous strong curved setae; flagellar joints cylindrical irregularly nodose 120-180 µm long, (joints 3rd to 5th the longest) with numerous setae arranged in irregular whorls, longest about two times as long as joint wide, include hair-like and fleshy setae and antennal bristles (minute setae associated with large setae have not been noted), apical joint bears a group of about 12 setae about as long as joint wide that apparently include a few antennal bristles only slightly thicker than other setae (other antennal sensilla not noted). Prothorax shrunken, hidden within mesothorax; prescutum transversely oval; details of scutum not visible; scutellum triangular, separated from mesopostnotum by a large membrane; mesosternum large, medial ridge not recognized; other thoracic structures obscure. Legs relatively large, 930-1080 µm long; coxa ca 120, femur 270-300, tibia 330-450, tarsus 120-150 µm, claw about 30 µm long; femur with a few small setae, tibia and tarsus with numerous conspicuous setae about as long as segment width (bifurcate setae not noted), femur with a group of minute apical setae; tarsal digitules not differentiated; claw narrow, slightly bent, with 2 capitate digitules longer than claw. Only base of right wing preserved, with the proximal portion of subcostal ridge and posterior flexing membrane present; alar lobe with pocket well developed. Halteres leaflike, ca 140 µm, long, 55 µm wide, with 2 or 3 setae each. Abdomen distorted, apparently flattened dorsoventrally and twisted; tapered, with numerous short setae, except 6th tergite which bears 2 lateral groups of conspicuous setae; 7th tergite with numerous needlelike setae or some other minute structures; sternite with long medial setae. Penial sheath long 290 µm, 48 µm high at base, slightly curved downward, with a few needlelike setae and a group of cupolae on apex. Aedeagus

not visible. Near the penultimate abdominal segment there is a bundle of about 15 thin rods that may be wax products of the tail producing glands, detached from the abdomen. If correctly interpreted, the structures on 7th tergite may be tubular ducts.

**Note.** The compound eyes and triangular scutellum indicate that *Hammanococcus* is a member of the superfamily Orthezioidea, closest to the Coelostomidiidae Morrison 1928 with which it shares the lack of abdominal fleshy tassels; however, the legs are devoid of bifurcate setae

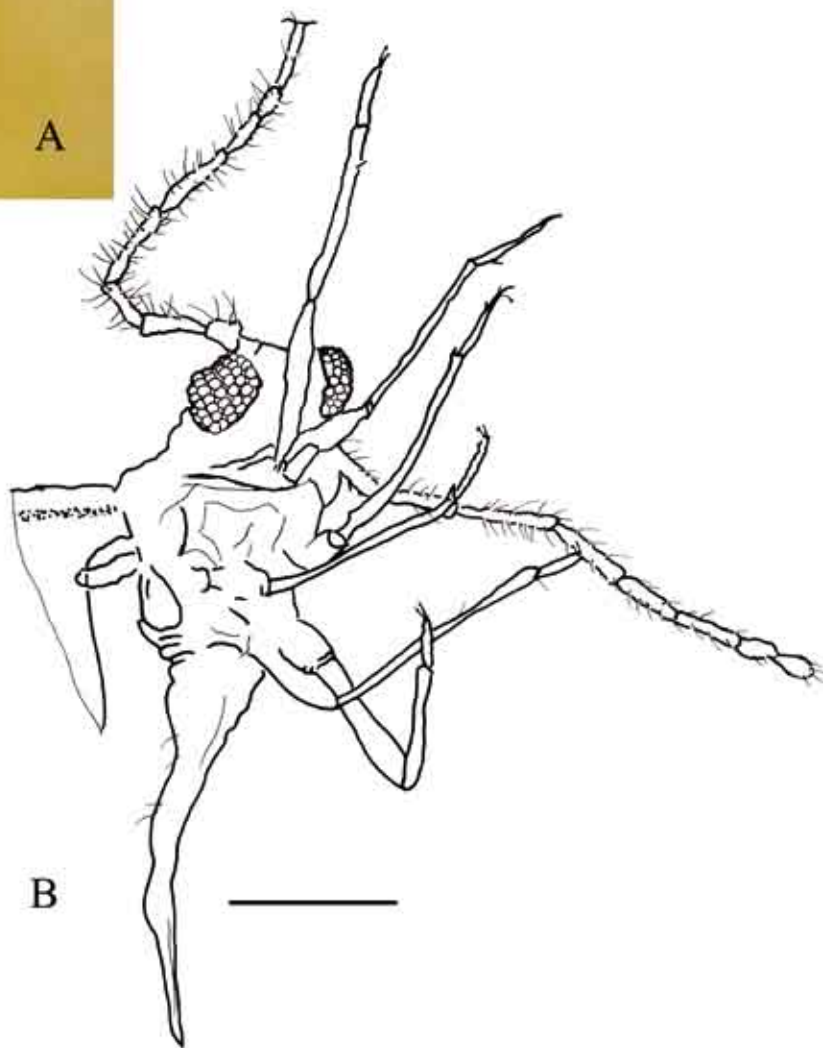
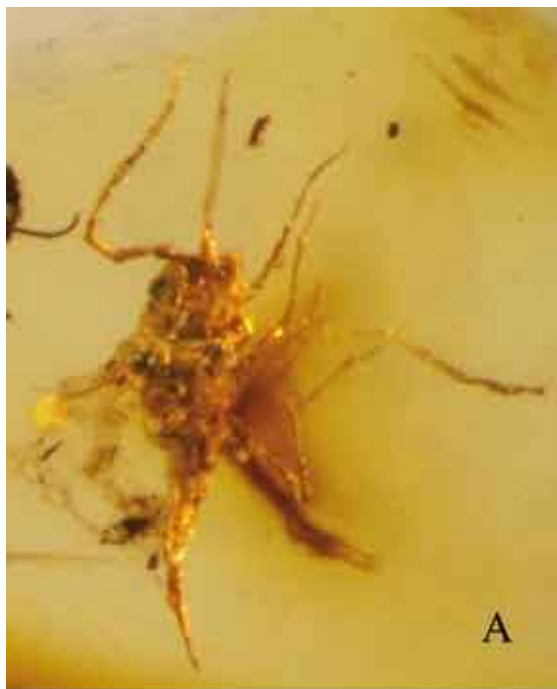


Plate 3: *Hammanococcus setosus* gen. et sp. n., holotype n HAM-555E (Cocc-1317c). Fig.A : Photography of *Hammanococcus setosus* gen. et sp. n., ventral view. Fig. B : Drawing of *Hammanococcus setosus* gen. et sp. n., ventral view. Scale bar represents 0.3 mm.

characteristic of this family and of Monophlebidae Signoret 1875. Also it differs from the Coelostomidiidae by the shape of haltere - bar-like in Coelostomidiidae, leaflike in *Hammanococcus* (this type occurs in the Monophlebidae). The penial sheath is similar in *Hammanococcus* and *Ultracoelostoma dracophylli* Morales as shown by Morales (1991).

Of particular interest is the structure of the abdomen. Although distorted, it apparently is flattened dorsoventrally, tapered and "prolonged" into the narrow penial sheath; fleshy tassels or any other lateral projections are absent. However, the 6th segment bears two marginal groups of conspicuous setae (2 setae in each group), whereas 7th sternite long thin medial setae. On 7th tergite there are minute structures which either may be setae or tubular ducts producing waxy rods in various archeococcid groups (but not in the monophlebid or coelostomidiids). Actually, there is a bundle of thin rods (filaments) near the apex of abdomen which may be part of the detached tail tuft. If so, *Hammanococcus* would have some relation with the Margarodidae s. str.

GENUS: *Hammanococcus* sp., larva

(Plate 4, figures A and B)

Among the Lebanese inclusions there are two larvae of considerable size and coelostomidiid-monophlebid appearance. It has been assumed that they may be related to the *Hammanococcidae*.

**Material examined.** Larva, specimen number HAM-475 (Cocc-1354), Larva, specimen number HAM-593 (Cocc-1580); Azar collection, housed provisionally in the Muséum National d'Histoire Naturelle, Paris. No other specimens available.

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Description.** (based on both specimens). Body flat, parallelsided, with rounded apices, 1.200 µm long, 450 µm wide. Antennae inserted on frontal margin, close together, six-segmented, short, thick, 310 µm long; all joints cylindrical, except apical which is club-shaped but with acute tip; length of segments (in µm): I - 30, II - 60, III to V each 30 (i.e., shorter than broad), VI - 130; scape with a few short setae, pedicel with numerous setae about as long as the width of joint, flagellar joints each with a circle of setae as long as segment wide or slightly longer, apical segment with very numerous setae up to 60 µm long, some setae are stouter than other, but a distinction of various types of sensilla and their number was impossible. Eyes conspicuous, protruding, about 40 µm in diameter. Labium (visible only under small magnification of stereoscope) apparently 3-segmented, conical, pointed, inserted slightly behind anterior coxae; a large portion of piercing stylets protrudes from its apex. Legs strong, but difficult to be measured owing to oblique positions and fungal hyphae; forefemur at least 210 µm long, combined length of hind-tibia, tarsus



Plate 4 : *Hammanococcus* sp., larva. Fig. A: Photography of *Hammanococcus* sp., larva, dorsal view, specimen HAM-475 (Cocc-1354). Fig. B: Photography of *Hammanococcus* sp., larva, dorsal view, specimen HAM-593 (Cocc-1580).

and claw 210  $\mu\text{m}$ , tarsus apparently shorter than tibia; setae on femur short, not numerous, on tibia and tarsus strong, exceeding their width; tibia with a group of setae on apex, but not evident spurs; tarsus with at least 12 setae, but no digitules; claw slender, almost straight, without denticles; unguis digitules setiform about 1/3 the length of claw. Body setae numerous (clearly visible on margins only) hairlike, inserted on small elongate cones of the characteristic monophlebid type, 30-90  $\mu\text{m}$  long. Groups of short (10-20  $\mu\text{m}$ ) conical spines have been noted but on three posterior abdominal segments, marginally. Anal lobes slightly protruding (which may be an artifact), each with a conspicuous apical seta 360  $\mu\text{m}$  long; a pair of setae slightly longer than body setae (120  $\mu\text{m}$ ) inserted medially. Anal opening, spiracles, cicatrices and cuticular pores invisible.

**Note.** The most striking feature of this inclusion is its complete overgrowing by hyphae of a fungus which occur in the whole amber piece. Basing on recent conditions, it is a saprophytic fungus which, however, does not preclude that the coccid was killed by a parasitic fungus. It seems to be very likely that the specimen was already dead and dried out when entombed in resin. The exposed piercing stylets support this suggestion.

The specimen apparently is a larva, most likely of the second stage, but perhaps not of the "preadult" one (6-segmented antennae). Descriptions of this instar are sparse in the recent species, in the archeococcids almost non-existing. The Matsucoccidae Morrison 1928, Xylococcidae Pergande 1898, Steingeliidae Morrison 1927, Margarodidae Cockerell 1899 and similar groups can be precluded as potential relatives of this specimen because of the high specialization of the crawler and apodeous larvae of older stages. Basing on the large size and coelostomidiid-monophlebid appearance it has been tentatively included in *Hammanococcus* although direct arguments for this placement are lacking.

Family: *Lebanococcidae* fam. nov.

Type genus *Lebanococcus* gen. nov.

**Diagnosis.** Male Archeococcids with compound eyes; triangular scutellum; very short, 8-segmented antennae, with short setae on all joints, antennal bristles and knobbed setae on apical joint; large mesosternum with well developed medial ridge; legs short, with several knobbed tarsal digitules, claw without denticle and digitules; wing oval, alar lobe protruding, finely sculptured, subcostal ridge narrow, reaching 2/3 wing length, traces of pterostigma recognizable, cubital ridge reduced, anterior flexing patch present, posterior one absent; abdomen cylindrical, tapering, of telescopic structure; Penial sheath tubular.

GENUS: *Lebanococcus* gen. nov.

Type species: *Lebanococcus longiventris* sp. nov., alate male

**Etymology.** The generic name refers to Lebanon in which the inclusion bearing amber was found. Grammatical gender: masculine.

**Diagnosis.** Small archeococcid, with compound eyes inserted laterally; well developed triangular middorsal and midventral plates; short, 8-segmented antennae, all antennal joints subequal in length, with short setae, apical joint with antennal bristles and knobbed setae; transversely oval prescutum, solid scutum, triangular scutellum, mesopostnotum separated from scutellum by a large membrane; mesosternum with medial ridge; legs short, tarsus 1/3 the length of tibia, with 5 knobbed digitules, claw small without denticle and digitules; wing oval, narrow at base, but with a well developed alar lobe, membranous, finely sculptured, subcostal ridge reaching 2/3 wing length, hypodermal pterostigma hardly recognizable, cubital ridge apparently reduced, anterior flexing membrane present, posterior absent; abdomen cylindrical, narrow, tapered, with 6 well defined segments arranged telescopically and a conspicuous peculiar terminal tube.

*Lebanococcus longiventris* sp. nov.

(Plate 5, figures A-C)

**Etymology.** Species name (Latin) refers to the long and narrow abdomen.

**Holotype.** Alate male, specimen number HAM-140C (Cocc-1315), Azar collection, housed provisionally in the Muséum National d'Histoire Naturelle, Paris. No other specimens available.

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Diagnosis.** As for the genus.

**Description.** Minute winged male 1020  $\mu\text{m}$  long, including "terminal tube", 190  $\mu\text{m}$  wide at mesothorax. Head broad, 115  $\mu\text{m}$  wide, well separated from thorax; ventromedial plate large, triangular, with midcranial ridge; dorsomedial plate of similar structure, but indistinct; compound eyes conspicuous, 60  $\mu\text{m}$  in diameter, accommodated at the sides of head; ocelli not noted; antennae 210  $\mu\text{m}$  long, shorter than wing width, 8-segmented; flagellar joints subequal in length (apical one slightly longer), with short hardly visible "usual" setae, apical joint tapered toward end, with one or two short antennal bristles (thin-walled pegs), four capitate setae and a few "usual" setae. Prothorax shrunken, but triangular sclerites can be seen anterior to forecoxae (which either may be interpreted as the ventral plate of head); prescutum transversely oval, strongly bulged; scutum apparently solid (without medial membrane); scutellum triangular, 65  $\mu\text{m}$  long, 70  $\mu\text{m}$  wide; between scutellum and mesopostnotum there is a broad membrane; mesosternum large, with a strong medial ridge; metasternum triangular (apparently metafurca). Legs relatively short, ca 300  $\mu\text{m}$  long, with small setae; tibia 130-150  $\mu\text{m}$ , much longer than tarsus, 50-55  $\mu\text{m}$ ; latter with 5 capitate digitules; claw small without digitules and denticles. Wings oval, with costal margin almost straight, narrow basally but with conspicuous alar lobes for holding hamuli, finely sculptured, apparently without microtrichia ("dots" visible

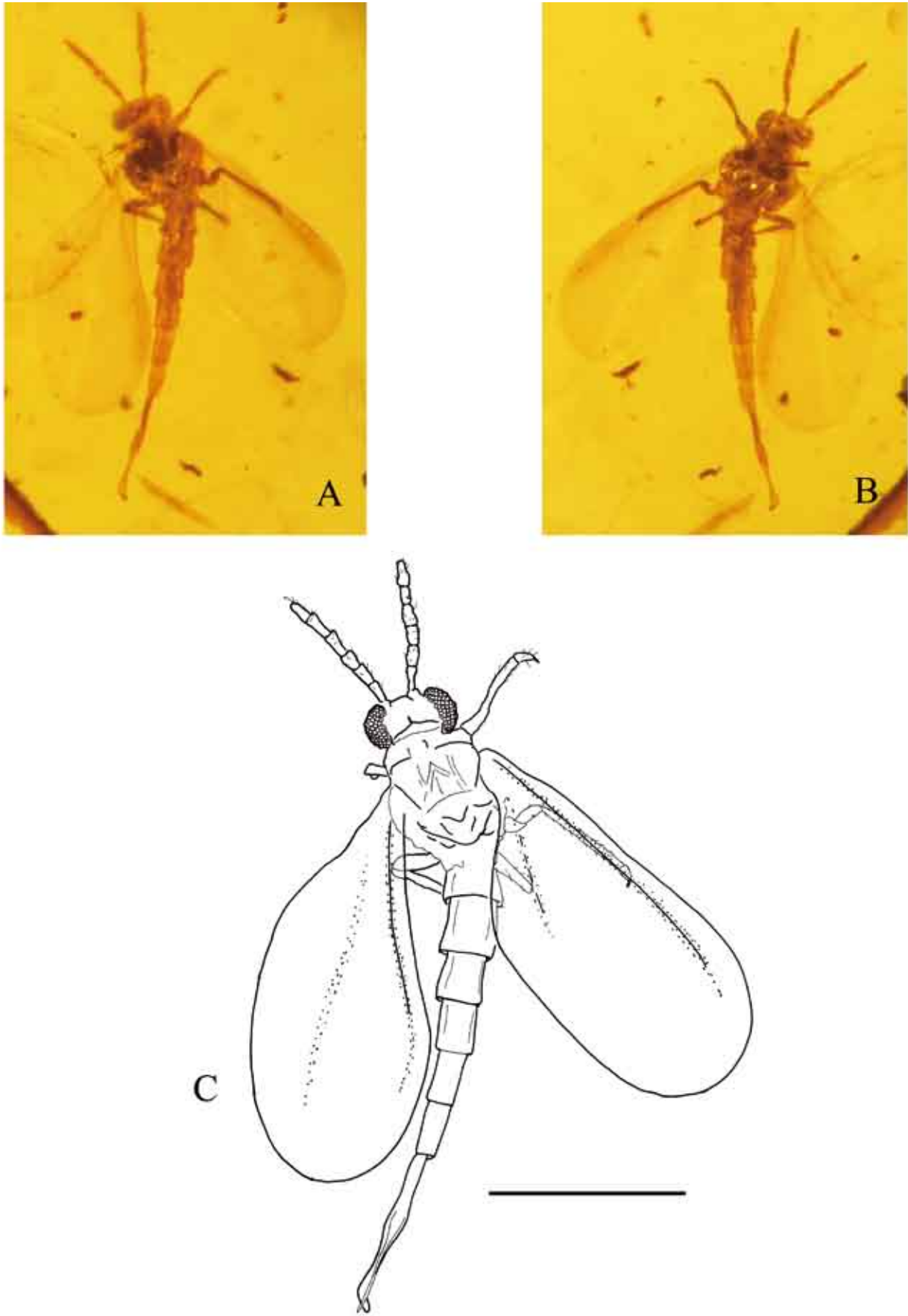


Plate 5: *Lebanococcus longiventris* gen. sp. n., alate male, holotype n HAM-140C (Cocc-1315). Fig. A: Photograph of *Lebanococcus longiventris* gen. sp. n., dorsal view. Fig. B: Photograph of *Lebanococcus longiventris* gen. sp. n., ventral view. Fig. C: Drawing of *Lebanococcus longiventris* gen. sp. n., dorsal view. Scale bar represents 0.3 mm.

on various parts of wing membrane supposedly are part of the relief); subcostal ridge narrow and short, extending to about 2/3 wing length; the anterior wing margin is slightly darker suggesting the presence of a hypodermal pterostigma; cubital ridge apparently completely reduced; anterior flexing line hardly recognizable, posterior one absent. Halteres clubshaped, setae not noted. Abdomen peculiar, cylindrical, tapered, with 6 distinct segments of telescopic structure (450  $\mu\text{m}$ ), and a narrow "terminal tube" (265  $\mu\text{m}$  long) in which three parts, subequal in length, can be recognized, the first, narrow, may be segment VII, the second, somewhat bulged, the segment VIII, and the third

one - an exposed endophalus (but a different interpretation also is possible, see "Notes").

**Notes.** The compound eyes, triangular scutellum and anterior flexing patch on wing indicate that *Lebanococcus* is a member of the superfamily Orthezioidea. The structure of the head corresponds, in general, with the conditions in the Ortheziidae, Matsucoccidae and Xylococcidae. However, the presence of alar lobes with a pocket for holding hamuli precludes these families as potential relatives of *Lebanococcus*. A triangular scutellum occurs in Margarodidae, Monophlebidae, Coelostomidiidae and the Cretaceous Grimaldiellidae

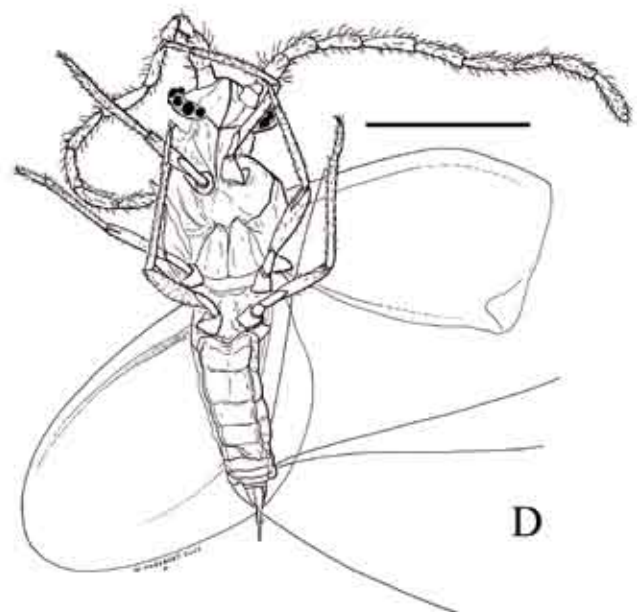
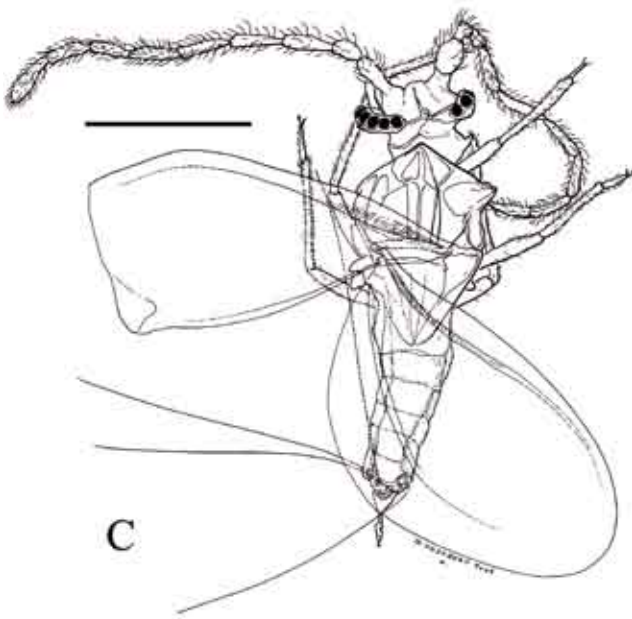


Plate 6: *Palaeosteingelia acrai* gen. et sp. n., male, holotype HAM-413A (Cocc-855a). Fig. A: Photography of *Palaeosteingelia acrai* gen. et sp. n., dorsal view. Fig. B: Photography of *Palaeosteingelia acrai* gen. et sp. n., ventral view. Fig. C: Drawing of *Palaeosteingelia acrai* gen. et sp. n., dorsal view. Scale bar represents 0.3 mm. Fig. D: Drawing of *Palaeosteingelia acrai* gen. et sp. n., ventral view. Scale bar represents 0.3 mm.

Koteja 2000 (Koteja 2000b), but other features are quite different. The numerous capitata tarsal digitules and very short antennae are unique in the archeococcids. A telescopic abdomen occurs in at least the gallforming recent *Opisthoscelis* sp. (Theron 1968) and *Callococcus leptospermi* (Maskell

1893) (Affi & Kosztarab 1967), described as *Sphaerococcus tomentosus* Fuller 1899, (consult also Williams & Miller 1999), both neococcids, but the apex of the abdomen is definitely different. The division of the “terminal tube” into three parts is not at all evident (it can be an artefact), but is based

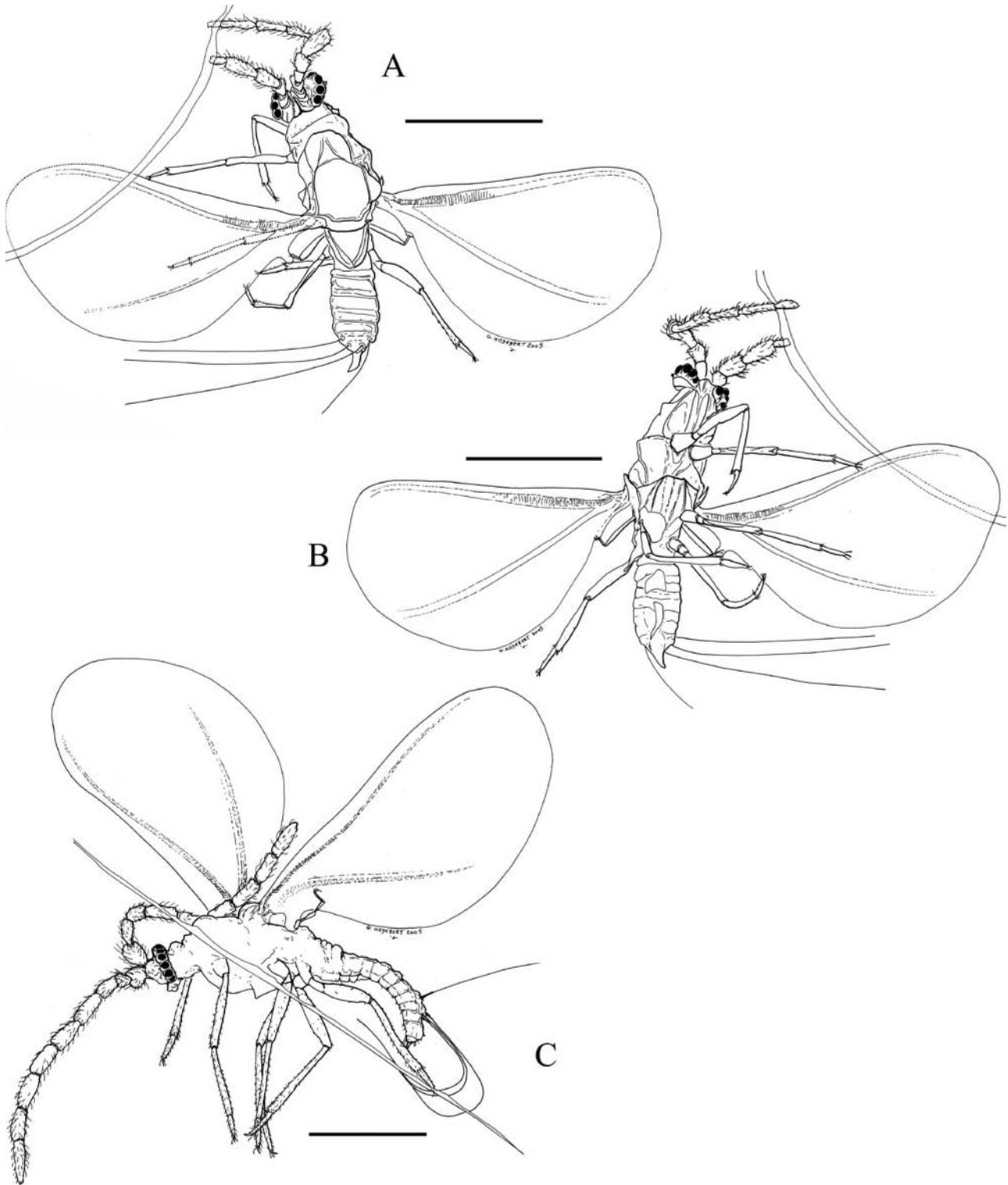


Plate 7: *Palaeosteingelia acrai* gen. et sp. n. Fig. A: Drawing of *Palaeosteingelia acrai* gen. et sp. n., dorsal view, paratype HAM-413B (Cocc-855b). Scale bar represents 0.3 mm. Fig. B: Drawing of *Palaeosteingelia acrai* gen. et sp. n., ventral view, paratype HAM-413B (Cocc-855b). Scale bar represents 0.3 mm. Fig. C: Drawing of *Palaeosteingelia acrai* gen. et sp. n., lateral view paratype HAM-413C (Cocc-855c). Scale bar represents 0.2 mm.

on the conditions in other male scale insects in which eight pregenital segments can be counted. The last part would then be a very simplified penial sheath, and the apical “thorn” - the aedeagus - or all an everted endophalus or even a bundle of spermatophores. In any case, the peculiar structure of the

abdomen seems to be an adaptation for mating with a gall inhabiting female.

Concluding, *Lebanococcus* may be considered a representative of an extinct archeococcid group of uncertain relationship, but with several derived and unique features.

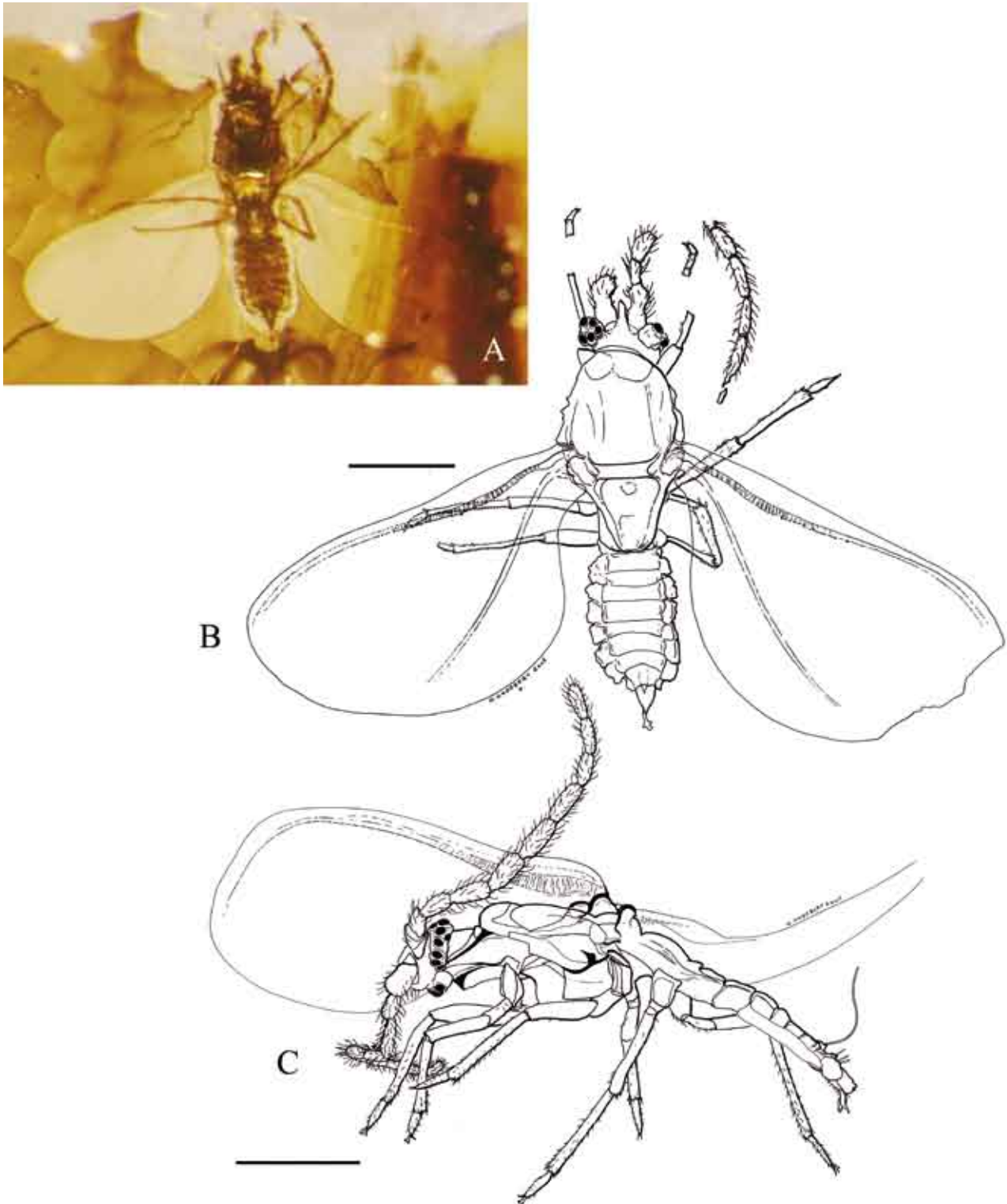


Plate 8: *Palaosteingelia acrai* gen. et sp. n. Fig. A: Photograph of *Palaosteingelia acrai* gen. et sp. n., dorsal view, paratype HAM-44 (Cocc-846). Fig. B: Drawing of *Palaosteingelia acrai* gen. et sp. n., dorsal view, paratype HAM-44 (Cocc-846), scale bar represents 0.2 mm. Fig. C: Drawing of *Palaosteingelia acrai* gen. et sp. n., lateral view, paratype HAM-409 (Cocc-851), scale bar represents 0.2 mm.

Family: Steingeliidae Morrison 1927

GENUS: *Palaeosteingelia* gen. nov.

Type species: *Palaeosteingelia acrai* sp. nov., alate male

**Etymology.** Palaeo (Latin) - ancient, and the generic name *Steingelia*. Grammatical gender: feminine.

**Diagnosis.** Steingeliid with broad wings (width: length ratio ca 1:1.8-1:2; 1:2.4 in *Steingelia*), ocular sclerites broadly separated dorsally and ventrally (adhering ventra-

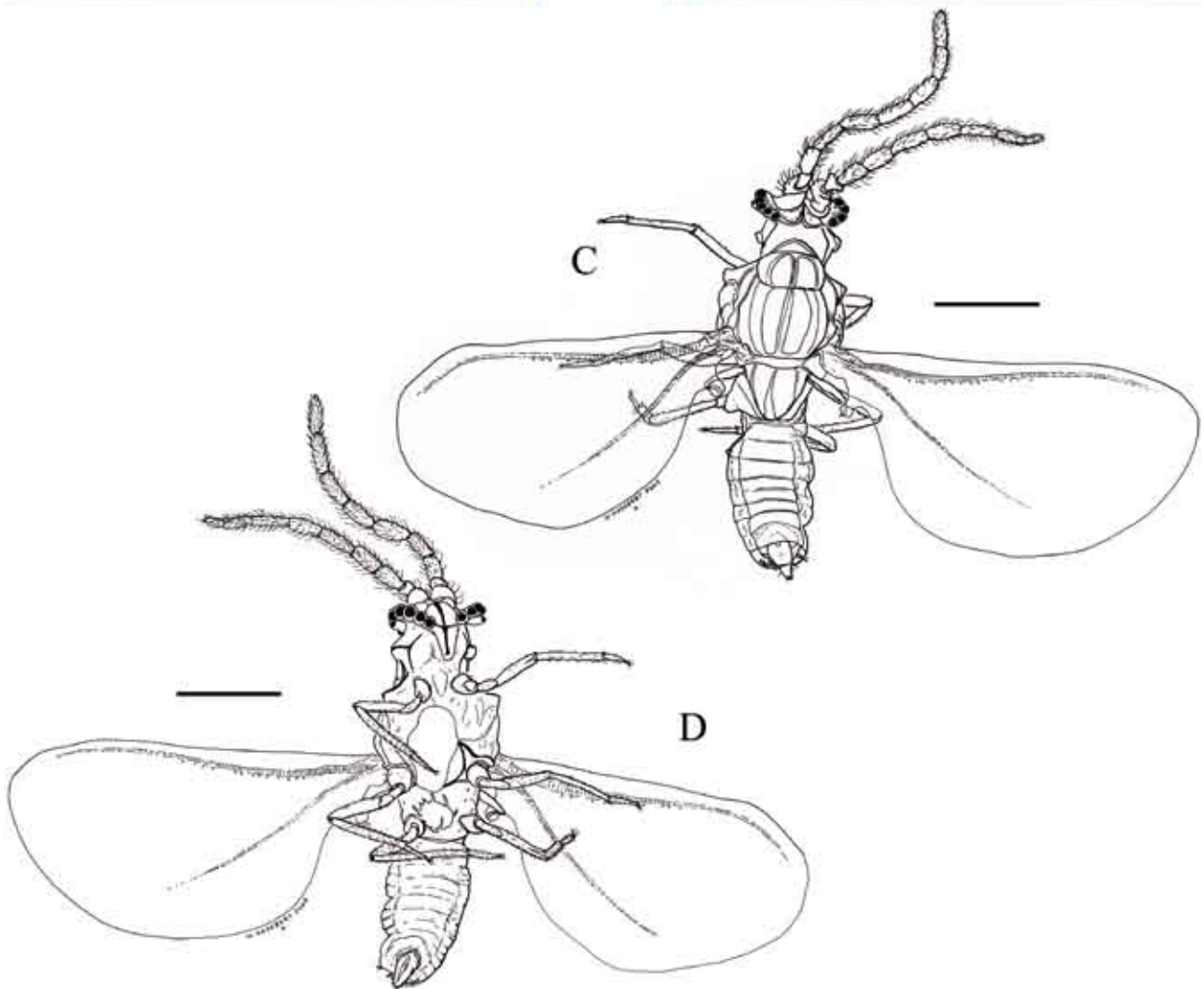


Plate 9: *Palaeosteingelia acrai* gen. et sp. n. Fig. A: Photography of *Palaeosteingelia acrai* gen. et sp. n., dorsal view, paratype HAM-410 (Cocc-0852). Fig. B: Photography of *Palaeosteingelia acrai* gen. et sp. n., ventral view, paratype HAM-410 (Cocc-0852). Fig. C: Drawing of *Palaeosteingelia acrai* gen. et sp. n., dorsal view, paratype HAM-410 (Cocc-0852), scale bar represents 0.2 mm. Fig. D: Drawing of *Palaeosteingelia acrai* gen. et sp. n., ventral view, paratype HAM-410 (Cocc-0852), scale bar represents 0.2 mm

lly in *Steingelia*), short first flagellar segment, very large rectangular membrane on scutum (small triangular in *Steingelia*) and more than one pair of tail waxy rods (one pair in *Steingelia*).

The two included species can be distinguished by the number of tail rods: two pairs in *P. acrai*, three or four pairs in *P. caudata*.

*Palaeosteingelia acrai* sp. nov.

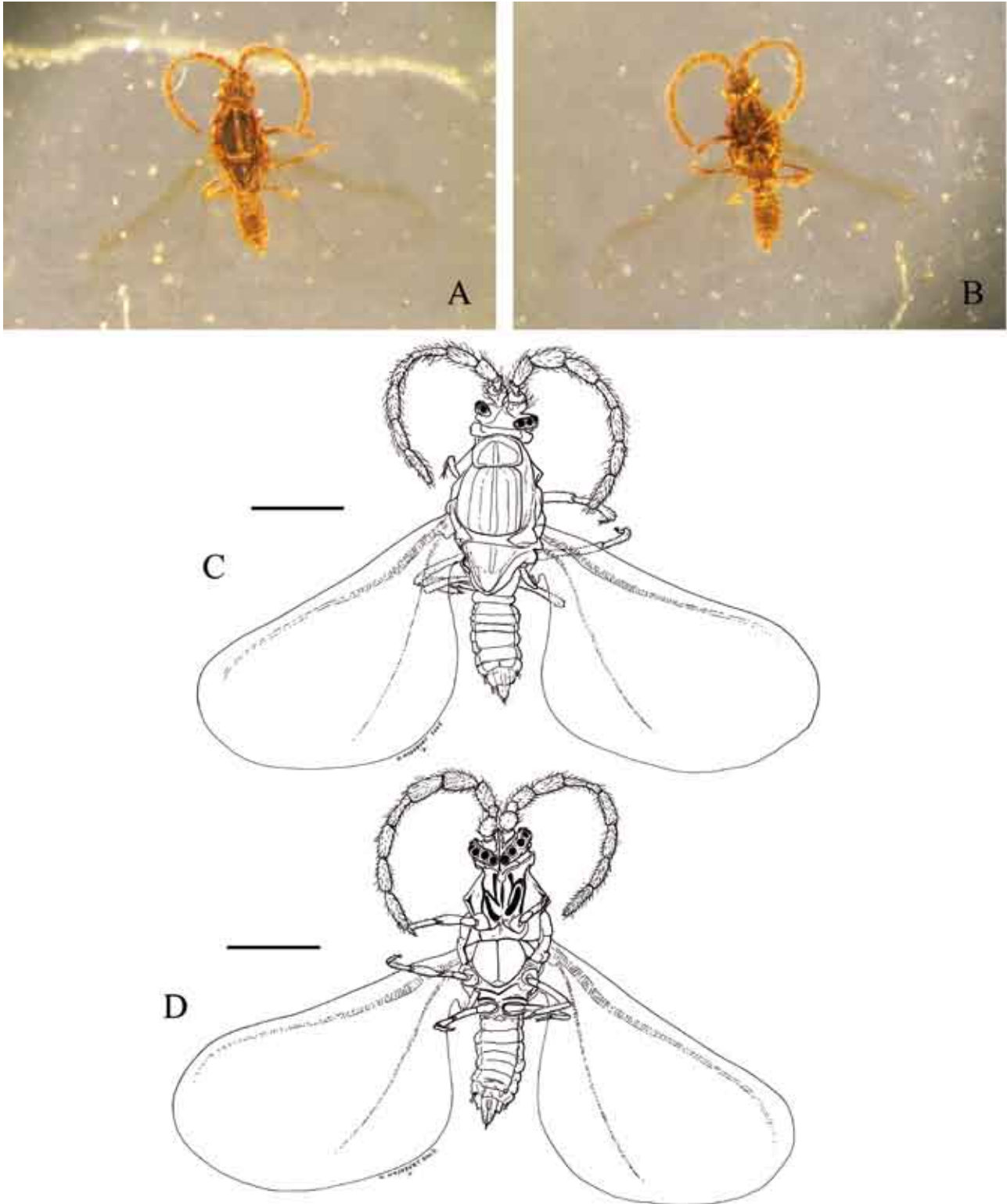


Plate 10: *Palaeosteingelia acrai* gen. et sp. n. Fig. A: Photograph of *Palaeosteingelia acrai* gen. et sp. n., dorsal view, paratype HAM-411 (Cocc-0853). Fig. B: Photograph of *Palaeosteingelia acrai* gen. et sp. n., ventral view, paratype HAM-411 (Cocc-0853). Fig. C: Drawing of *Palaeosteingelia acrai* gen. et sp. n., dorsal view, paratype HAM-411 (Cocc-0853), scale bar represents 0.2 mm. Fig. D: Drawing of *Palaeosteingelia acrai* gen. et sp. n., ventral view, paratype HAM-411 (Cocc-0853), scale bar represents 0.2 mm.

(Plates 6-11)

**Etymology.** The species is named in honour of the late Prof. Aftim Acra

**Holotype.** Alate male, specimen number HAM-413A (Cocc-0855a), Azar collection, housed provisionally in the Muséum National d'Histoire Naturelle, Paris, see plate 6, figs A-D

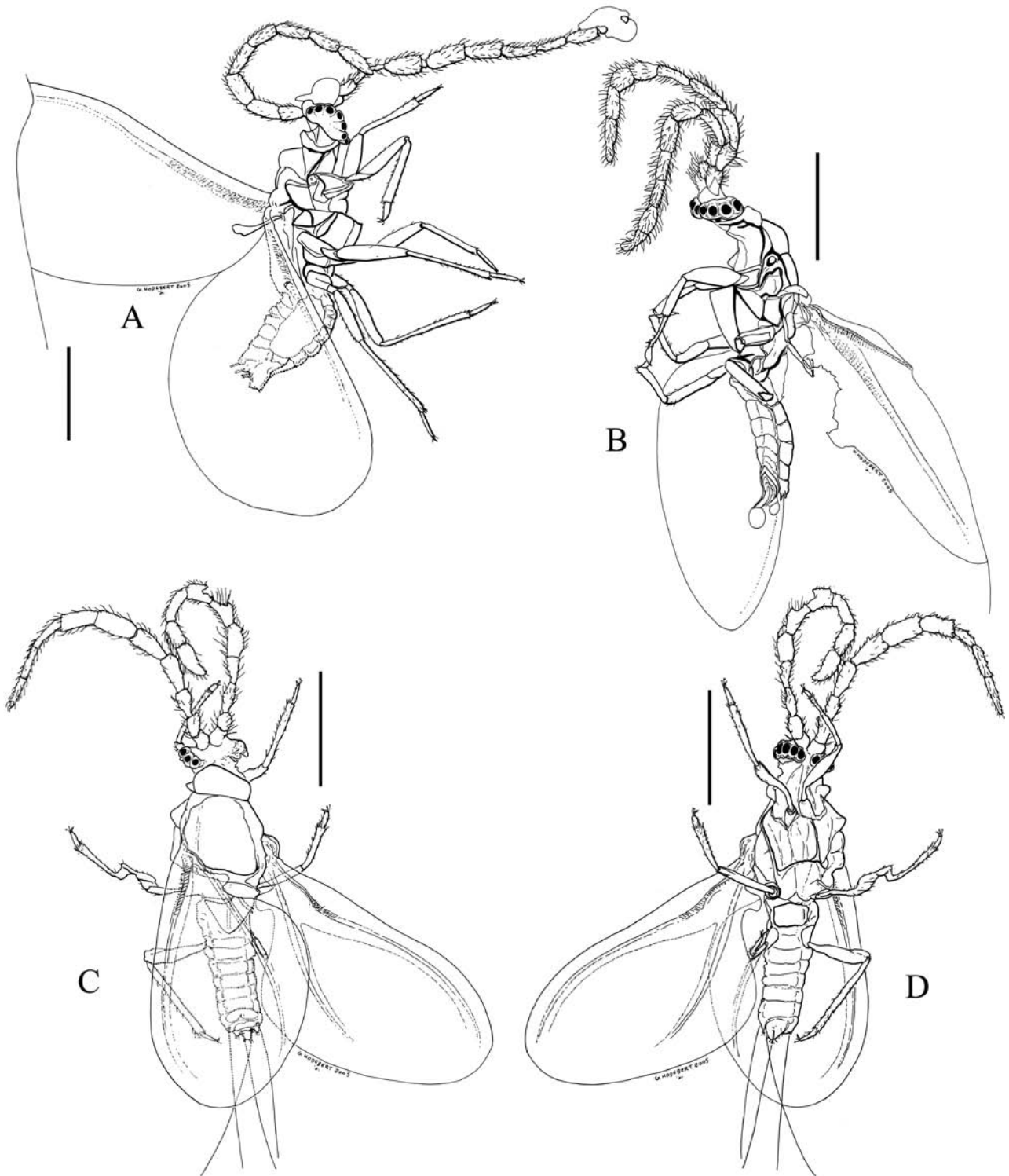


Plate 11: *Palaeosteingelia acrae* gen. et sp. n. Fig. A: Drawing of of *Palaeosteingelia acrae* gen. et sp. n., lateral view, paratype HAM-412 (Cocc-0854), scale bar represents 0.2 mm. Fig. B: Drawing of of *Palaeosteingelia acrae* gen. et sp. n., lateral view, paratype HAM-415A (Cocc-0857), scale bar represents 0.2 mm. Fig. C: Drawing of *Palaeosteingelia acrae* gen. et sp. n., dorsal view, paratype HAM-580 (Cocc-1318), scale bar represents 0.3 mm. Fig. D: Drawing of *Palaeosteingelia acrae* gen. et sp. n., ventral view, paratype HAM-580 (Cocc-1318), scale bar represents 0.3 mm.

**Paratypes.** (all males): specimens' number: HAM-413B&C (Cocc-0855b-c) (see plate 7, figs A-C) ; HAM-44 (Cocc-0846) plate 8, figs A and B; HAM-409 (Cocc-0851) plate 8, fig. C; HAM-410 (Cocc-0852) plate 9, figs A-D; HAM -411 (Cocc-0853) plate 10, figs A-D; HAM -412 (Cocc-0854) plate 11, fig. A; HAM -414 (Cocc-

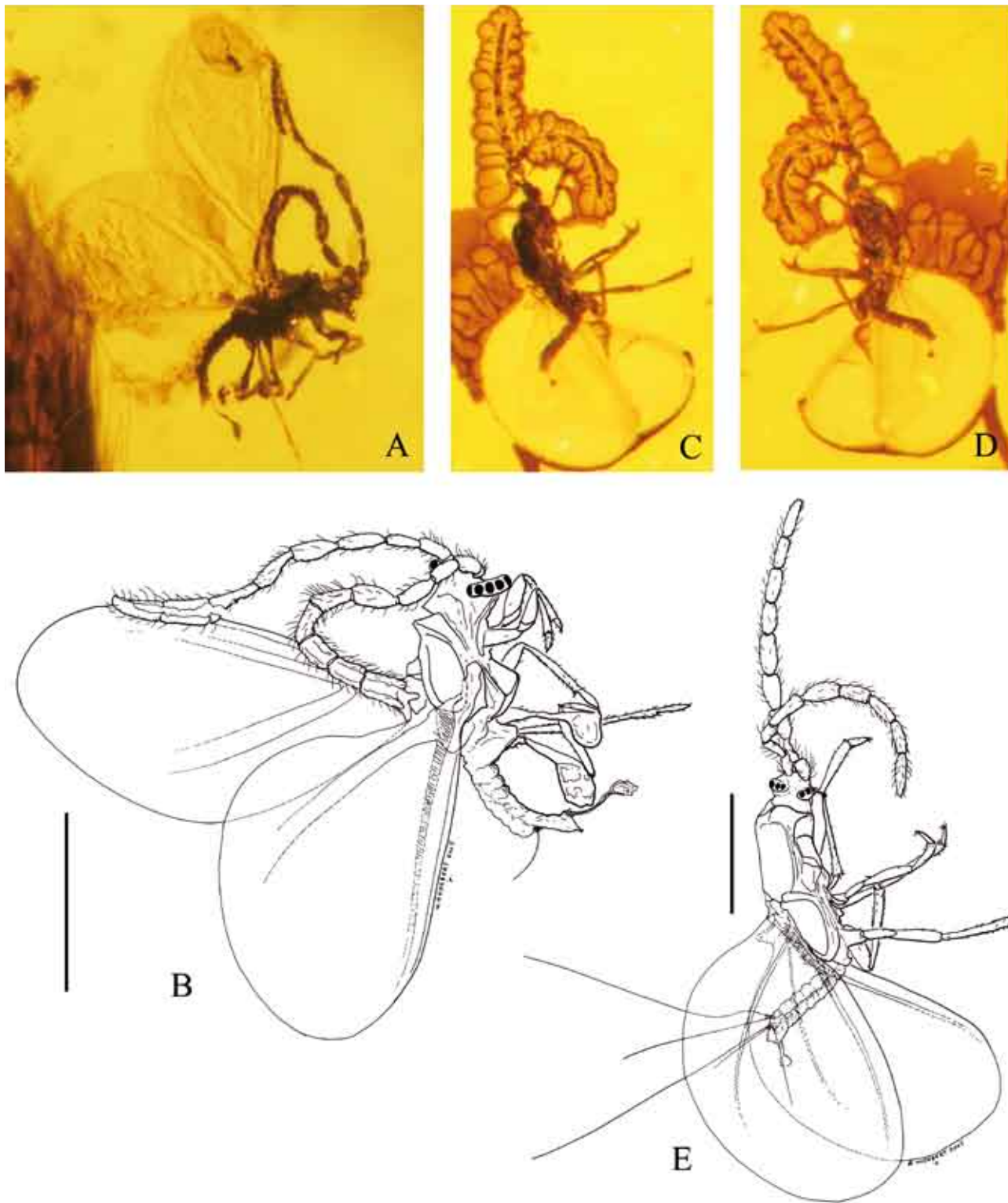


Plate 12: *Palaeosteingelia caudata* gen et sp. n. Fig. A: Photography of *Palaeosteingelia caudata* gen et sp. n., lateral view, holotype HAM-418 (Cocc-0860a). Fig. B: Drawing of *Palaeosteingelia caudata* gen et sp. n., lateral view, holotype HAM-418 (Cocc-0860a), scale bar represents 0.3 mm. Fig. C: Photography of *Palaeosteingelia caudata* gen et sp. n., right lateral view, specimen HAM-416 (Cocc-0858). Fig. D: Photography of *Palaeosteingelia caudata* gen et sp. n., left lateral view, specimen HAM-416 (Cocc-0858). Fig. E: Drawing of *Palaeosteingelia caudata* gen et sp. n., right lateral view, specimen HAM-416 (Cocc-0858), scale bar represents 0.3 mm.

0856); HAM -415A (Cocc-0857) plate 11, fig. B; HAM -417 (Cocc-0859); HAM -580 (Cocc-1318) plate 11, figs C and D; HAM -581 (Cocc-1319); HAM -584 (Cocc-1322); HAM -585 (Cocc-1323); HAM -592A (Cocc-1579).

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Diagnosis.** As for the genus.

**Description.** (based on all specimens, for measurements of individual specimens see table 2). Minute winged males 600-900 µm long (apparently shrunken), 200-300 wide at mesothorax, with distinct constriction at metathorax. Head short, broad, clearly separated from prothorax, with strong ocular sclerites separated dorsally and ventrally, bearing, each, 7 simple eyes and an ocellus (this number is not always evident on the inclusions). Dorsomedial and ventromedial plates well developed, triangular, with

cha/in	HAM-Cocc-	44 846	409 851	410 852	411 853	412 854	413A 855a	413B 855b	413C 855c	414 856	415A 857	417 859	580 1318	581 1319	584 1322	585 1323	592A 1579
body l		840	810	900	660	660	840	690	690	660	690	600	750	600	870	630	-
body w		240	-	300	210	-	260	130	-	180	-	210	240	-	240	-	-
head l		-	-	-	-	65	-	-	-	-	-	-	-	-	-	60	-
head w		150	-	220	160	-	235	132	-	144	-	-	180	-	210	-	-
no. e.		-	7	7	?6	-	-	-	-	?7	7	?6	?6	?6	?6	-	-
ant l		-	665	-	-	760	803	-	-	-	-	-	794	-	802	-	-
sc		-	-	-	-	-	35	-	-	42	-	30	-	-	-	-	-
pd		-	-	-	-	-	78	-	-	42	-	48	65	-	66	60	-
f1		-	55	-	-	72	60	-	48	60	42	42	60	-	42	54	-
f2		-	66	90	78	84	90	-	-	78	78	72	96	60	96	78	-
f3		-	78	90	84	90	96	-	72	90	90	84	100	78	90	78	-
f4		-	84	90	90	90	96	-	72	-	-	78	102	78	108	60	-
f5		-	78	90	78	84	84	-	66	-	-	72	96	66	90	66	-
f6		84	60	90	78	78	78	-	66	-	-	-	90	60	90	66	-
f7		84	66	96	72	72	78	-	60	-	-	-	60	78	84	72	-
f8		84	78	90	90	90	108	-	84	84	-	-	90	90	102	-	-
prs l		66	-	78	72	-	78	54	-	48	-	-	90	-	-	-	-
prs w		132	-	150	120	-	120	90	-	120	-	-	138	-	-	-	-
scu l		150	-	150	144	-	120	132	-	102	-	-	-	-	-	-	-
scl l		30	-	25	25	-	25	25	-	24	-	18	25	-	-	-	-
scl w		132	-	138	132	-	120	110	-	102	-	90	150	-	-	-	-
win l		720	?660	792	678	-	660	672	630	-	-	-	720	?480	850	720	-
win w		390	?360	450	330	-	360	360	312	-	-	-	390	-	450	360	-
hal l		96	-	120	90	96	-	96	96	-	84	-	108	?90	120	84	-
hal w		?18	-	18	-	18	-	12	12	-	12	-	12	12	12	12	-
forel l		-	456	-	-	444	-	420	-	-	-	-	-	-	450	-	-
forel cox		-	60	-	-	-	-	-	-	-	-	-	-	60	-	-	-
forel t+f		-	156	?168	-	168	-	138	-	-	-	-	-	138	150	-	-
forel ti		-	174	?168	-	150	180	162	162	-	-	-	180	150	180	150	-
forel ta		-	66	78	-	66	66	60	60	-	-	-	60	60	60	82	-
midl l		-	474	-	-	504	-	-	-	-	-	-	-	-	-	492	-
midl cox		-	-	-	-	-	-	-	-	-	-	-	-	-	66	66	-
midl t+f		180	?168	180	-	168	162	162	-	-	-	-	180	?120	174	138	-
midl ti		-	?180	?180	-	192	168	-	-	-	-	-	-	?132	174	144	-
midl ta		-	66	84	-	84	72	-	-	-	-	-	-	60	78	72	-
hindl		-	522	564	-	510	-	-	-	-	-	-	-	-	504	-	-
hindl cox		-	60	-	-	60	-	-	-	-	-	-	-	-	60	60	-
hindl t+f		180	?168	180	-	168	168	162	?120	156	-	-	198	?120	174	132	-
hindl ti		198	?210	240	-	210	210	168	162	180	-	162	240	?16	186	168	-
hindl ta		-	84	84	-	72	78	60	60	90	-	-	-	-	84	72	-
ps l		90	84	96	78	-	78	84	-	-	-	-	66	60	?102	78	-
w		72	-	54	36	-	48	48	-	-	-	-	54	-	?60	48	-
tail		4	4	4	-	4	4	4	4	4	4	-	4	-	4	4	-

Table 2. Measurements (in µm) in *Palaeosteingelia acraei*. Abbreviations: ? - uncertain data; "-" - no data; ant - antenna; cha/in - characteristic/number of inclusion; cox - coxa; f1-8 - flagellar segments 1-8; forel - foreleg; hal - haltere; hindl - hindleg; l - length; midl - midleg; no. e - number of pairs of simple eyes; ped - pedicel; prs - prescutum; ps - penial sheath; sc - scape; scl - scutellum; scu - scutum; t+f - trochanter+femur; ta - tarsus; tail - number of tail filaments; ti - tibia; w - width; win - wing.

distinct midcranial ridge. Antennae 10-segmented, 650-800  $\mu\text{m}$  long; scape much shorter than pedicel (50-60  $\mu\text{m}$  long, both with numerous setae; first flagellar segment the shortest (40-60  $\mu\text{m}$  long), third, fourth and apical segments the longest (70-100  $\mu\text{m}$ ); all segments with numerous uni-

form setae, slightly longer than segment width, capitate setae and distinct antennal bristles not observed.

Prothorax membranous, with dorsal, lateral and ventral sclerites present (as described by Theron 1958). Prescutum transversely oval, 70-90  $\mu\text{m}$  long, 120-140  $\mu\text{m}$  wide; all

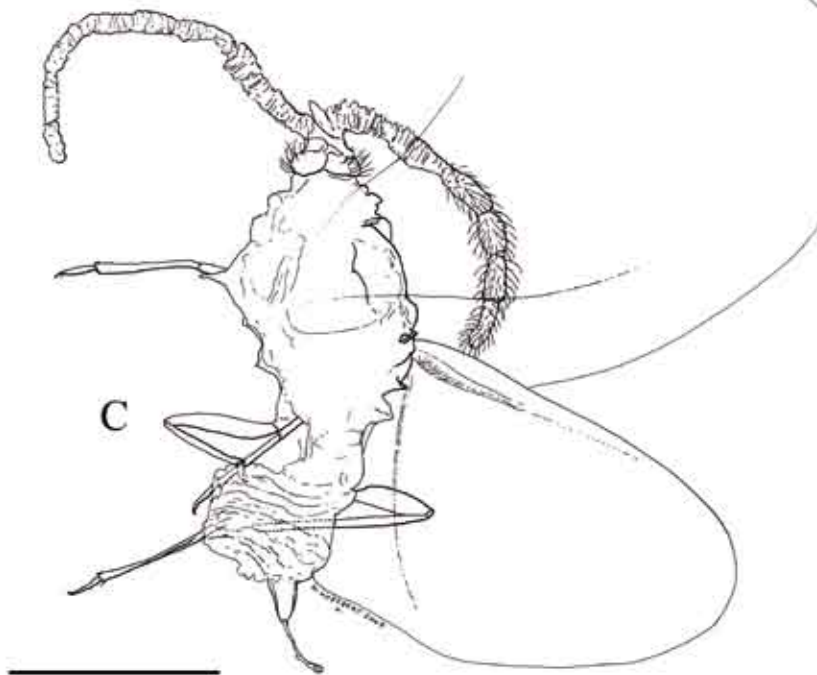
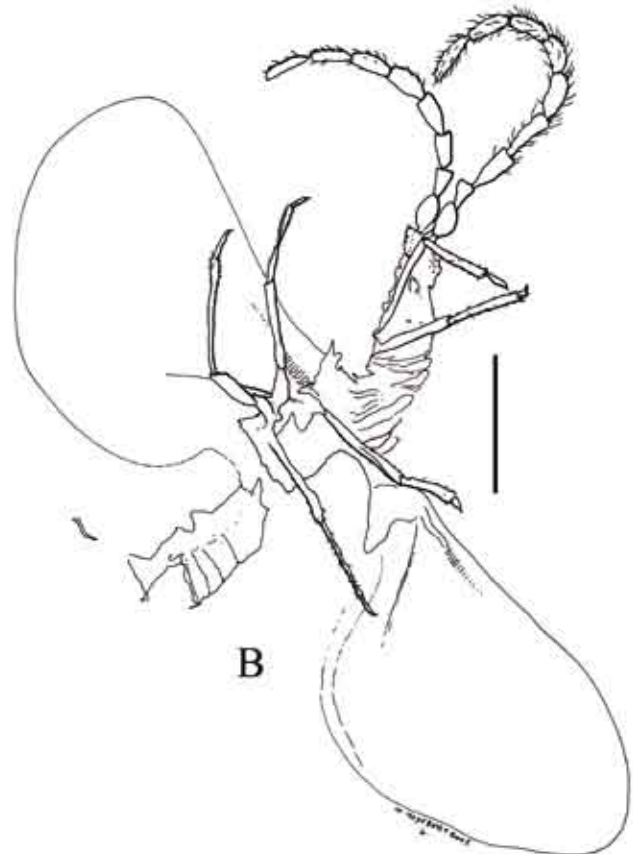


Plate 13: *Palaeosteingelia* sp. Fig. A: Photograph of *Palaeosteingelia* sp, specimen HAM-555D (1317b). Fig. B: Drawing of *Palaeosteingelia* sp, specimen HAM-555D (1317b). Scale bar represents 0.3 mm. Fig. C: Drawing of *Palaeosteingelia* sp, specimen HAM-555B (1317a). Scale bar represents 0.3 mm.

medial part of scutum from prescutum to scutellum membranous, much longer (100-150 µm) than prescutum; scutellum tubular, strongly sclerotized, very short, about 25 µm long, 100-140 µm wide, without foramen. Mesopostnotum and mesopostphragma extended far into abdomen, the

membrane between scutellum and mesopostnotum about as long as mesonotum. Mesosternum with medial ridge; furcal pit large.

Legs slender, with all joint distinct, with numerous short setae, 450-500 µm long; coxa about 60 µm,

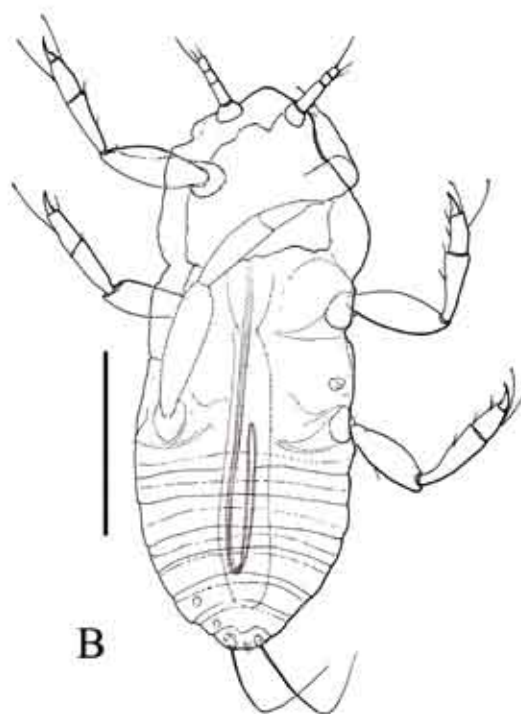


Plate 14: ?*Palaeosteingelia* sp. Fig. A: Photography of ?*Palaeosteingelia* sp., larva (crawler), ventral view, specimen HAM-86 (Cocc-0848). Fig. B: Drawing of ?*Palaeosteingelia* sp., larva (crawler), ventral view, specimen HAM-86 (Cocc-0848), scale bar represents 0.1 mm. Fig. C: Photography of ?*Palaeosteingelia* sp., larva (crawler), dorsal view, specimen HAM-594 (Cocc-01581). Fig. D: Photography of ?*Palaeosteingelia* sp., larva (crawler), ventral view, specimen HAM-594 (Cocc-01581)

trochanter+femur 160-180, tibia 160-240 (with a group of apical spurs), tarsus 60-80  $\mu\text{m}$  long, with a pair of capitate digitules; claw slender, without teeth and digitules.

Wings broad, 650-850  $\mu\text{m}$  long, 350-450  $\mu\text{m}$  wide; with well developed alar lobe for holding halteral setae; with fine polygonal sculpture, without microtrichia; subcostal ridge reaching 3/4 wing length, cubital ridge distinct, but without cuticular bar, both flexing patches lacking. Halteres parallelsided, 90-120  $\mu\text{m}$  long, about 15  $\mu\text{m}$  wide, with 2 hamuli.

Abdomen cylindrical (in almost all inclusions flattened), membranous, with a few short setae and two pairs of dorsolateral wax tail producing organs on two posterior abdominal segments. The structure of these organs has not been recognized in any inclusions; however, in all instances the organs consist of two short subequal (ca 20  $\mu\text{m}$  long) setae that run parallelly, about 3  $\mu\text{m}$  apart, without any other accessory setae. Sometimes they make an impression as being the wall of a tubular duct, and it is not clear whether they, or some invisible glands at their base, produce the waxy filament. In both the Recent *Steingelia gorodetskia* Nasonov, 1908 and the New Jersey amber *S. cretacea* Koteja, 2000 the tails are produced by multilocular pores at the base of the tail setae (three in number and of different size) which support the waxy rods, i. e., corresponding with the conditions in the neococoids. In some instances the waxy filaments have been preserved, attaining at least the length of abdomen; also, they are "soft" and flexible (straight in the neococoids). Waxy tails similar to those in *Palaeosteingelia acraei* (considering number and features) have been observed in *Kukaspis usingeri* from Alaskan amber; however, the bases of the tails were not accessible for examination in this inclusion (Koteja & Poinar 2001).

Penial sheath conical, rounded apically, perhaps membranous, with short dorsal setae and much longer ventral setae. Aedeagus sickle-like, acute, short. Often sperm can be noted on its apex.

***Palaeosteingelia caudata* sp. nov.**

(Plate 12, figures A-E)

**Etymology.** "Caudatus" (Latin) = bearing a tail.

**Holotype.** Alate male, specimen number HAM-418A (Cocc-0860a), Azar collection, housed provisionally in the Muséum National d'Histoire Naturelle, Paris, plate 12, figs A and B.

**Paratype.** Specimen's number: HAM-418B (Cocc-0860b); syninclusion of holotype.

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Other material examined.** HAM-416 (Cocc-0858); alate male; other data as given for type material, plate 12, figs C-E.

**Description.** (holotype). As far as characteristics can be recognized and described in amber preserved scale insects, these specimens could quite well be placed in *P. acraei*, if not the four pairs of waxy tails. In extant forms, the num-

ber of tail organs is constant in species and genera, and even higher taxa; e. g., in mealybugs, representatives of the Pseudococcinae Cockerell, 1905 bear one pair of tails, whereas those of the Phenacoccinae Šulc, 1944, two pairs. Basing on this evidence, the abundant material of Lebanese *Palaeosteingelia* has been placed within two species. However, in the mealybugs the two pairs of tails arise from two segments, whereas in *P. caudata* the "additional" tails seem to originate from the same segments, i. e., each of the two posterior abdominal segments bears four tails. For measurements see table 2.

In HAM-416 (Cocc-0858), only six tails have been observed, thus it has been excluded from the type series of *P. caudata*.

***Palaeosteingelia* sp.**

(Plate 13, figures A-C)

**Material examined.** HAM-36 (Cocc-0845), alate male; HAM-555B plate 13 fig. C and HAM-555D (Cocc-1317a-b) plate 13 fig. A and B, alate males. Other coccid syninclusions: HAM-555E (Cocc-1317c)- holotype of *Hammanococcus setosus*, this paper.

Features that would allow identification of these specimens have not been preserved.

**?*Palaeosteingelia* sp., larva (crawler)**

(Plate 14, figures A-D)

There are two crawlers in the Lebanese amber similar to the recent steingeliids; however, since the diagnose of *Palaeosteingelia* is based on adult male, the specimens cannot be placed in this genus.

**Material examined.** HAM-86(Cocc-0848), larva (crawler) plate 14, figures A and B; and HAM-594 (Cocc-01581), larva (crawler); plate 14, figures C and D.

**Description** (based on both specimens). Body 300  $\mu\text{m}$  long, 120  $\mu\text{m}$  wide, flat, parallelsided, front rounded, posterior apex tapered, with a pair of apical setae 36  $\mu\text{m}$  long, inserted close each other. Eyes conspicuous. Antennae inserted ventrally, apart from each other; very short (35  $\mu\text{m}$ ) and slender compared with the body and legs, their distal joints seem to be removed during preparation, but this is not evident. Clypeus and labium not recognizable (latter seems to be located between midlegs); loop of piercing stylets seems to return toward hind coxae after reaching body end. Legs subequal in size (120  $\mu\text{m}$ ), thick; trochanter and femur seem to be fused, 55  $\mu\text{m}$  long; tibia broadened distally, with apical spurs, 30  $\mu\text{m}$  long; tarsus (25  $\mu\text{m}$  long) with a few short setae and long knobbed tarsal digitules (24  $\mu\text{m}$ ); claw strong, digitules not recognized. Spiracles and anal opening not visible.

This specimen is an archeococcid crawler, most similar to *Steingelia*, distinct from it by the conspicuous tarsal digitules (absent in *Steingelia*), and lack of unguis digitules (present in *Steingelia*). The reason for which it has been affiliated with *Palaeosteingelia* is the large number of males found there. This obviously is a weak statistical argument.

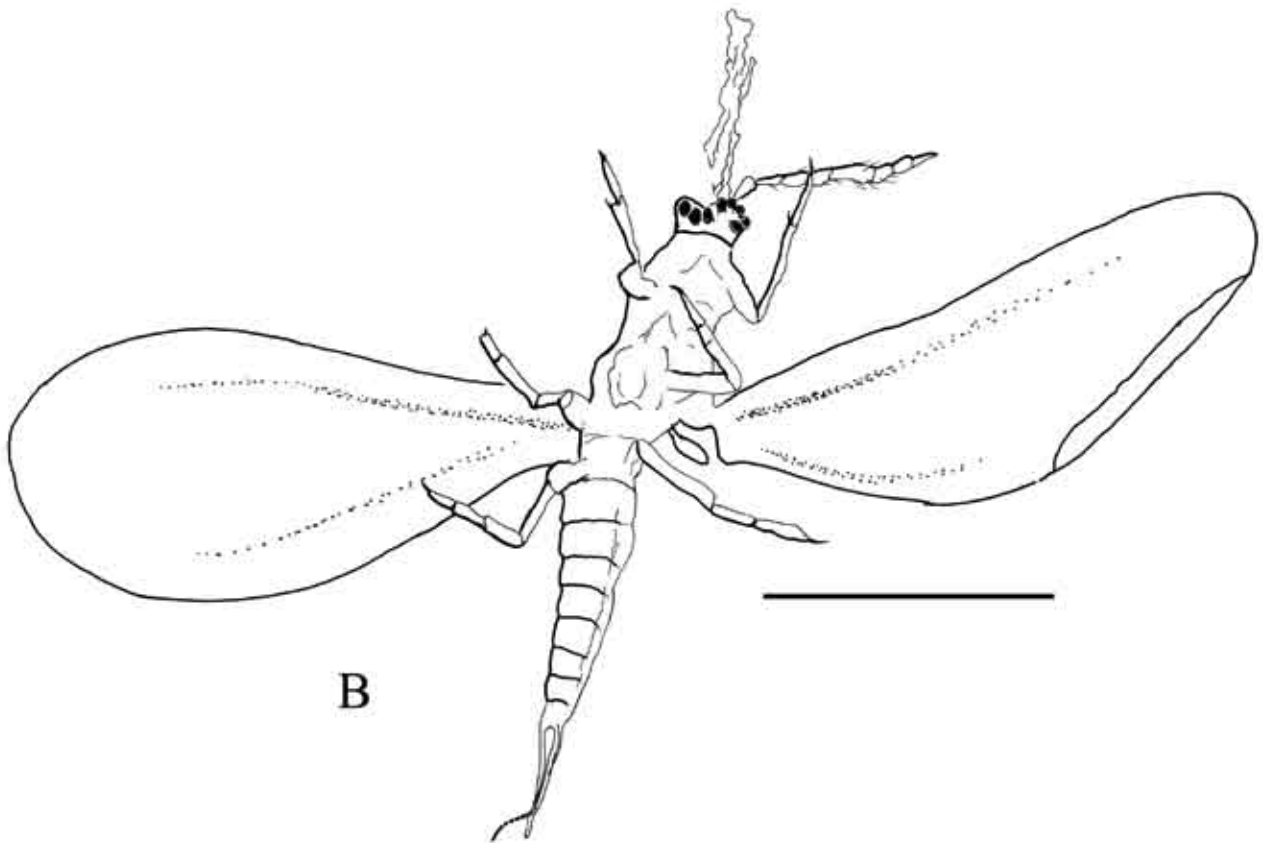


Plate 15: *Apticoccus minutus* gen et sp. n., alate male, holotype HAM-54A (Cocc-0847). Fig. A : Photography of *Apticoccus minutus* gen et sp. n., male, ventral view, Fig. B: Drawing of *Apticoccus minutus* gen et sp. n., male, ventral view. Scale bar represents 0.3 mm.

**Note.** The recent and fossil genus *Steingelia* Nasonov 1908 has been a subject of controversy since the discovery of its males by Green (1914), mainly because of the striking difference between the degree of specialization of female and male; the former retained archeococcid features, latter underwent morphological changes similar to those in the neococcids, however, retaining some archeococcid characteristics, e. g., lack of wing microtrichia (for review see Koteja 2000b). One of the characteristic features of *Steingelia* male is the translocation of the preoral ridge, mouth opening and tentorium far rearward into the prothorax, at the level of forecoxae (Theron 1958). Another marked steingeliid feature is the junction of ends of pronotal ridge with propleuron+cervical sclerites by means of sclerotized patches which form a strong support (“shoulders”) of prothorax, especially well visible in inclusions in which membranous parts of this body region significantly shrunk. Basing on these features, and the general similarity, the fossils in questions have been formally affiliated with the Steingeliidae. The rearward shifting of the mouthparts into the thorax occurs already in the steingeliid crawler, but is characteristic of many other archeococcid groups, e. g., Xylococcidae Pergande, 1898, Matsucoccidae Morrison, 1928, Kuwaniidae MacGillivray, 1921, Margarodidae Cockerell, 1899 s. str. and Coelostomidiidae Morrison, 1927, (Morrison 1928, Koteja 1974b).

Another steingeliid feature worth mention are the digitules. Adult female *Steingelia gorodetskia* bears a bundle of unguis digitules (about 10), but no tarsal digitules. First stage larva and prepupa have only one pair of unguis digitules, second and third instar larvae are legless (Koteja & ak-Ogaza 1981). In male, unguis digitules are absent, but a pair of capitate tarsal digitules is well developed (misinterpreted as unguis digitules by Morrison 1928; cf. Koteja 2000b). In both *Steingelia cretacea* and *Palaeosteingelia* males, only one pair of knobbed tarsal digitules has been noted, but no unguis digitules. The larva HAM-86 (Cocc-0848) bears a pair of very long capitate tarsal sensilla, none unguis digitules, thus the objection of placing it to *Palaeosteingelia*.

The tail organs represent a difficult problem for interpretation. In both extant and fossil *Steingelia*, the tail is produced by a pair of a large laterodorsal clusters of multilocular pores associated with two or three conspicuous, variable in length, setae, devices corresponding with conditions in neococcids. In *Palaeosteingelia* 2-4 pairs of tails have been found, each associated with two equal short setae inserted close each other thus making an impression of a tube; multilocular pores have not been ascertained; however, if present, then forming a small cluster because the waxy tails are quite thin and “soft”. Judging from the tails (their bases and the devices that produced them were not accessible), similar structures may occur in the Alaskan amber *Kukaspiis* Koteja & Poinar 2001 (Koteja & Poinar 2001).

Finally, *Palaeosteingelia* is very abundant constituting 54 % of the Lebanese amber inclusions. In the Recent fauna, the Steingeliidae are represented by two monoty-

pic and apparently relict genera: *Steingelia gorodetskia* Nasonov 1908 throughout the Palearctic and *Stomacoccus platani* Ferris 1917 found only in one locality in the Nearctic (California); former feeding on roots of birch, latter on trunk of sycamore. It may reasonably be assumed that *Palaeosteingelia* lived on the resin producing tree. In this case we have to postulate a radical change of the host and feeding behaviour without significant structural modifications in the steingeliids.

Family: ?Electrococcidae Koteja 2000

#### GENUS *Apticoccus* gen. nov.

Type species: *Apticoccus minutus* sp. nov., alate male

**Etymology.** The generic name refers to ‘Aptian’ time in Lower Cretaceous. Grammatical gender: masculine

**Diagnosis.** Electrococcid-like minute male with 9-segmented antennae, not markedly enlarged pedicel, short caudal setae and narrow, long penial sheath.

*Apticoccus minutus* sp. nov.

(Plate 15, figures A-B)

**Etymology.** The male of this species is the smallest in the Electrococcidae.

**Holotype.** Alate male, specimen number HAM-54A (Cocc-0847), Azar collection, housed provisionally in the Muséum National d’Histoire Naturelle, Paris.

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Description.** Minute winged male about 680 µm long, 150 µm wide at mesothorax. Head deformed, 55 µm long, 80 µm wide, with at least 6 simple eyes and a large ocellus on each side. Sclerites difficult to see. Antennae deformed (right antenna decomposed), apparently 9-segmented, 250 µm long (i. e. much shorter than in *Electrococcus* Beardsley, 1969 and *Turonicoccus* Koteja 2000); pedicel about 50 µm, not markedly enlarged, apical joint slender, pointed; all joints with variable setae (apical joint with terminal bristle), capitate setae not noted. Scutellum tubular; basisternum large, without medial ridge, with conspicuous furcal pit. Other details not visible. Legs 760-850 µm long, coxa 85, femur+trochanter 290, tibia 300-360, tarsus with claw 100 µm long; all joints with short setae, tibia with apical spurs, tarsal digitules knobbed, much longer than claw, claw without digitules and teeth. Wings spoon-like, with narrow base, conspicuous alar lobe, 660 µm long, 330 µm wide, short subcostal and cubital ridges, no flexing patches, bearing microtrichia. Haltere spindle-shaped, 70 µm long, 20 µm wide, with one seta. Abdomen evenly tapered, with 4 caudal setae shorter than half length of penial sheath. Penial sheath narrow, tapered, straight, 90 µm long, 25 µm wide at base. Aedeagus tubular, flexible with acute apex.

**Note.** *Apticoccus* is similar to the New Jersey amber *Turonicoccus* and to the Canadian amber *Electrococcus*.

It is distinct from these genera by the following characteristics: (a) The antenna is shorter, 9-segmented, pedicel not markedly enlarged, apical segment much more slender than other joints, without capitate setae; (b) tarsal digitules knobbed, long (absent in *Electrococcus*); (c) lack of unguis

digitules (present in *Turonicoccus*); (d) 2 hamuli (one in *Turonicoccus*, haltere lacking in *Electrococcus*); (e) short caudal setae (very long in *Turonicoccus*, absent in *Electrococcus*); (f) long, slender penial sheath, width/length ratio 1/4 (1/2 and 1/3 in *Turonicoccus* and *Electrococcus* respec-

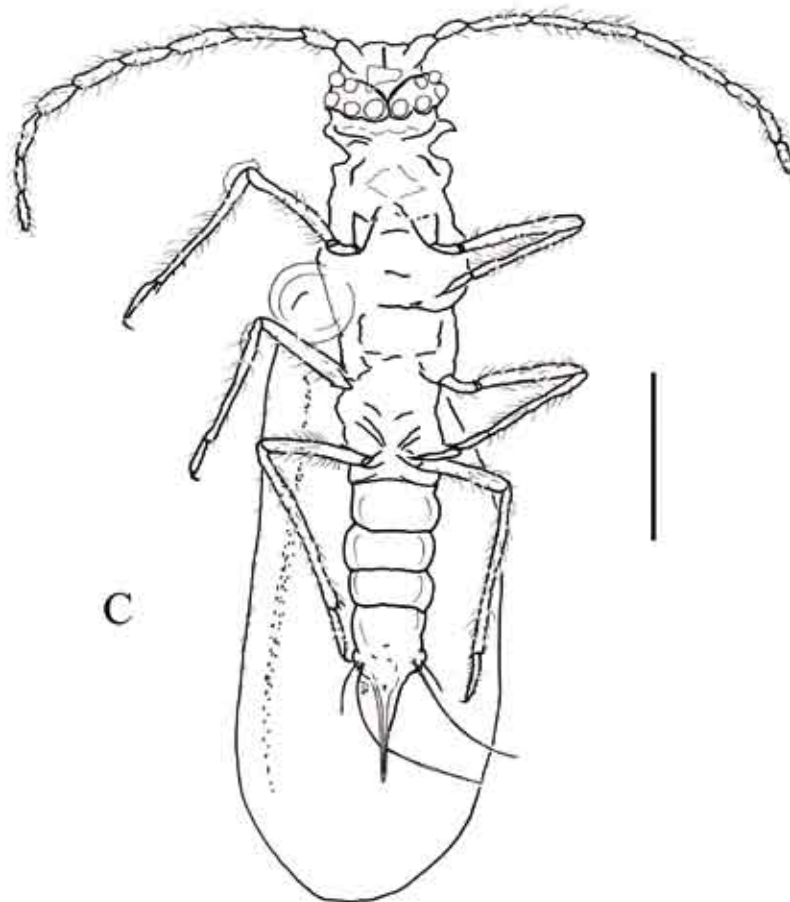
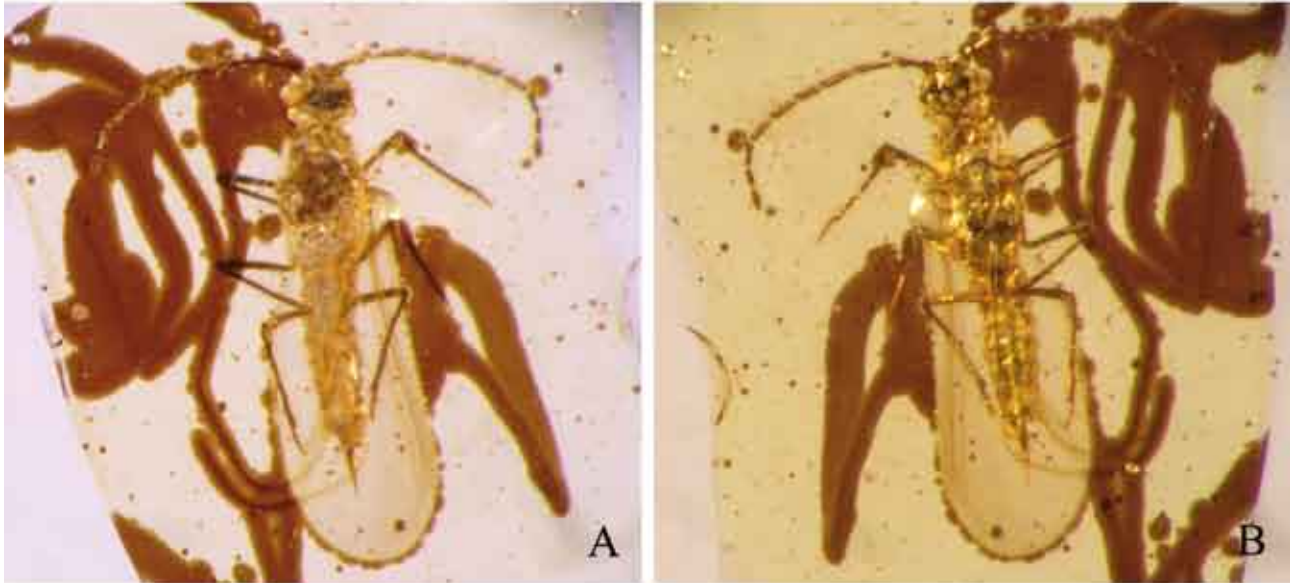


Plate 16: *Palaeotupo danieleae* gen et sp. n., alate male, holotype HAM-582 (Cocc-1320). Fig. A: Photography of *Palaeotupo danieleae* gen et sp. n., dorsal view. Fig. B: Photography of *Palaeotupo danieleae* gen et sp. n., ventral view. Fig. C: Drawing of *Palaeotupo danieleae* gen et sp. n., ventral view. Scale bar represents 0.3 mm.

tively). Currently, it is difficult to comment about the value of these differences, since only one specimen is available in both *Electrococcus* and *Apticoccus*. A markedly enlarged pedicel constitutes a diagnostic feature of *Electrococcidae* (Beardsley 1969, Koteja 2000b); in *Apticoccus* this feature is lacking, thus its inclusion in this family is tentative.

Superfamily: Coccoidea Fallén 1814

Family: ?Putoidae Beardsley 1969

GENUS: *Palaeotupo* gen. nov.

Type species: *Palaeotupo danieleae* sp. nov., alate male

**Etymology.** Palaeo (Latin) = ancient, and ‘tupo’ an anagram of the generic name *Puto*. Grammatical gender: masculine.

**Diagnosis.** Male putoid-like neococcid with two rows of simple eyes and knobbed setae on apical antennal joint, narrow penial sheath, and lacking claw digitules and teeth.

*Palaeotupo danieleae* sp. nov.

(Plate 16, figures A-C)

**Etymology.** Species named in honour of Dr Danièle Matile-Ferrero, her friendship and contribution to the knowledge of scale insects.

**Holotype.** Alate male, specimen number HAM-582 (Cocc-1320), Azar collection, housed provisionally in the Muséum National d’Histoire Naturelle, Paris. Inclusion well preserved, accessible from dorsum and venter, many details can be examined, but a splitting along the longitudinal body axis deforms somewhat the thorax from venter; left wing broken at base and removed, supposedly during entrapping

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Description.** Medium sized winged male about 1300 µm long, 300 µm wide at mesothorax, with mealy wax secretion on prothorax and abdomen. Head rotund, 240 µm long, 300 µm wide, with two rows of simple eyes, 3 pairs in anterior row and 4 pairs in posterior one, and a pair of ocelli, ocular sclerites strong apparently fused on venter; middorsal plate distinct, medial ridge not recognized; midventral plate with well developed, bifurcate at apex, medial ridge; a few short setae visible at apex of head. Antennae 10-segmented, 845-890 µm long (left antenna longer); scape conspicuous, 48-54 µm long, with a few short setae; pedicel similar to flagellar joints, 72 µm long, with at least 15 setae much longer than segment width; flagellar joints cylindrical, about 110-132, 110-114, 90-84, 102-90, 84-102, 84-90, 72-66, 72-84 µm, respectively (right antenna on first position); bearing numerous scattered setae (including antennal bristles, fleshy and hair-like setae, difficult to distinguish sometimes) about two times as long as segment with, and about 5 capitate setae at apex of terminal joint. Prescutum subpentagonal, with short setae,

scutum solid (without membrane), scutellum subtriangular, with one angle directed rearward; prothoracic sternites present, difficult to define. Legs strong, 775-880 µm long (posterior leg the longest), with numerous setae much longer than segment width, tibia with strong apical spurs; coxa 85-90 µm, femur+trochanter 275-295 µm, tibia 295-360 µm, tarsus 85-100 µm, without digitules; claw small, about 35 µm without denticles or digitules. Wings elongate oval, with straight costal margin, 1140 µm long, 480 µm wide, alar pouch for holding hamuli well developed, but small; wing membrane reticulated, with distinct microtrichia (alar sensilla not noted); venation of neococcid type, subcostal ridge paralleling wing margin, fades out far before reaching its apex, cubital ridge well developed, flexing membranes absent. Halteres bar-like, 110 µm, with 2 hamuli. Abdomen cylindrical, parallelsided, with a few short setae (well visible on pleural regions), dorsal ostioles not evident. Pre-genital segment with slightly protruding lateral projections, each with a glandular pouch, dorsally, and two setae about 360 µm long inserted at bottom of pouch, and two ventral seta (the longer 180 µm). Waxy tails well preserved, about as long as abdomen. Penial sheath conical, evenly tapered, 210 µm long, 60 µm wide at base, with a few setae on venter and sides. Aedeagus not visible.

**Note.** *Palaeotupo danieleae* apparently is a neococcid corresponding with the putoid-pseudococcid-eriococcid type, especially considering the solid scutum (without central membrane). Unique within all scale insects are the simple eyes arranged in two rows, as a form of ‘disintegration’ of the compound eyes. Tail organs resemble those of Putoidae Beardsley 1969, Pseudococcinae Cockerell 1905 and Eriococcidae Cockerell 1899, but there are very long seta on ventral face of the lateral projections not reported in the above groups. The penial sheath is definitely distinct from the putoid, pseudococcid, and eriococcid types (Reyne 1954, Afifi 1968), but shows some similarity with some genera of the Coccidae Fallén 1814, (Giliomee 1967). Capitate setae are present on apical flagellar joint, but digitules are absent on tarsus and claw (this is also devoid denticles). It is difficult to decide whether these differences, as well as the relative length of antennae, legs and wings, and the number and length of setae, are of generic or familial value. It seems that this fossil is a member of an extinct group of the neococcid lineage. Tentatively, it has been assigned in the Putoidae.

Family: Pennygullaniidae fam. nov.

GENUS: *Pennygullania* gen. nov.

Type species: *Pennygullania electrina* sp. nov., alate male

**Etymology.** Genus named in honour of Dr Penny Gullan and her contribution to the study of scale insects. Grammatical gender: feminine.

**Diagnosis.** Slim neococcid with two pairs of simple eyes, slender appendages bearing very long setae, solid scutum, trochanter and femur fused, two pairs of strong tail setae (with two setae in each group), penial sheath of coccid s. str. type.

*Pennygullania electrina* sp. nov.

(Plate 17, figures A-)

**Etymology.** Electron (Greek) - amber

**Holotype.** Alate male, specimen number HAM-381 (Cocc-0849), Azar collection, housed provisionally in the Muséum National d'Histoire Naturelle, Paris. Inclusion

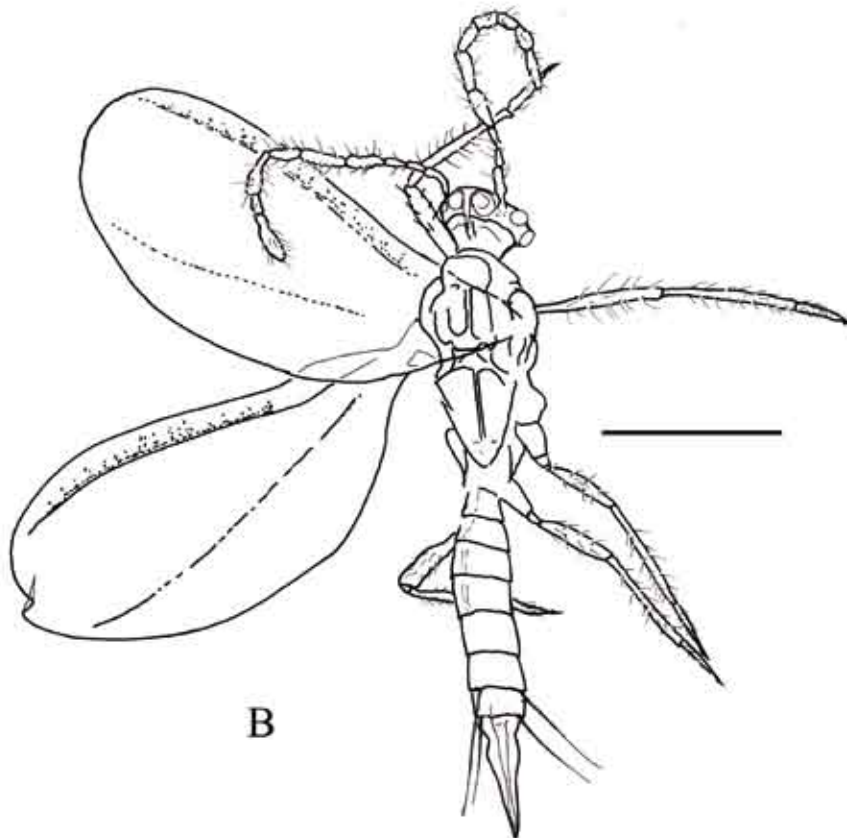


Plate 17: *Pennygullania electrina* gen et sp. n. and ?*Pennygullania* sp. Fig. A: Photography of *Pennygullania electrina* gen et sp. n., alate male, ventral view, holotype HAM-381 (Cocc-0849). Fig. B: Drawing of *Pennygullania electrina* gen et sp. n., alate male, dorsal view, holotype HAM-381 (Cocc-0849). Scale bar represents 0.3 mm. Fig. C: Photography of ?*Pennygullania* sp., larva, specimen HAM-583 (Cocc-1321).

completely impregnated with resin, body much deformed, thorax hidden beneath bubbles from venter.

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Description.** Body slender, 1170  $\mu\text{m}$  long, 230  $\mu\text{m}$  wide at mesothorax, without any wax secretion preserved. Head greatly deformed, but pre- and postocular and ventral midcranial ridges distinct; with two pairs of simple eyes, the dorsal and ventral ones, as in most neococcids, but the dorsal eyes are located very closely each other (artifact?); a few short setae visible at apex of head. Antennae 10-segmented, relatively short, about 650  $\mu\text{m}$  long; joints cylindrical (much deformed); scape 30  $\mu\text{m}$  long (setae not recognized), pedicel similar to flagellar joints, 70  $\mu\text{m}$  long, with a whorl of about 10 very long setae at apex; flagellar joints I-III and VIII 80-95  $\mu\text{m}$  long, the remaining 50-60  $\mu\text{m}$  long, bearing antennal bristles (on segments V-VIII), fleshy and hair-like setae (capitate setae not found), fleshy setae very long, about as long as the joints, arranged in one or two whorls. Prescutum oval, scutum apparently without medial membrane, structure of scutellum difficult to ascertain, supposedly risen, but apparently not triangular; venter of thorax hidden beneath bubbles. Legs slender, 660, 560 and 620  $\mu\text{m}$  long, respectively, with numerous very long setae, including coxae; coxa 65-70  $\mu\text{m}$  long, trochanter and femur apparently fused, 230-24  $\mu\text{m}$  long, tibia 215-230  $\mu\text{m}$  long, with strong apical spurs; tarsus one-segmented, 100-120  $\mu\text{m}$  long, with 2 knobbed digitules, slightly longer than claw, claw slender, without denticles, with 2 knobbed digitules about as long as claw. Wings elongate oval, with almost straight costal margin, 870  $\mu\text{m}$  long, 390  $\mu\text{m}$  wide, alar lobe with pouch for holding hamuli well developed, sclerotized marginally; wings hyaline (reticulation not recognizable), with long microtrichia (alar sensilla not noted); venation of neococcid type, subcostal ridge paralleling wing margin, fades out slightly before reaching wing apex, cubital ridge well developed, of about the same length, flexing membranes absent. Halteres bar-like, with costal ridge, 110  $\mu\text{m}$  long, with 1 hamulus. Abdomen cylindrical, parallelsided, slender, membranous (completely compressed on inclusion), with a few setae on each segment and "glandular" pouches on dorsal margins of two pregenital segments; two tail setae about 240  $\mu\text{m}$  long arise from each pouch, wax secretions (if actually produced) not preserved. Penial sheath conspicuous, conical, slightly bulged at base, evenly tapered to sharp apex, 200  $\mu\text{m}$  long, 60  $\mu\text{m}$  wide at base, with a few setae on venter and sides. Aedeagus as long as penial sheath, pointed, attached to a short basal rod.

**Note.** As far, *Pennygullania* is the only Cretaceous species bearing two pairs of simple eyes, as most of the recent neococcids. Unfortunately, because of the significant distortion of the head, it is difficult to recognize details of its structure, except that there are evident postocular ridges. Scutellum also is deformed. In general, the species reminds some Coccidae Fallén 1814, (e.g. *Inglisia*, c. f. *Giliomee* 1967), but the apex of abdomen is definitely different. Two

pairs of tail setae occur only in the Phenacocinae Šulc 1944 (Pseudococcidae Cockerell 1905) among the neococcids. However, it is not at all certain that the setae form a support of waxy threads; quite possible they alone form the tail. Penial sheath, apparently strongly sclerotized, is of coccid s. str. type, but its base is bulged, with a slight constriction between sheath and 8th abdominal segment (feature unique in scale insects). *Pennygullania* bears many derived features, and seems to represent a specialized branch of neococcids that became extinct during Cretaceous.

**?*Pennygullania* sp., larva**

This well preserved specimen apparently is a peculiar neococcid that cannot be placed in any extant group; it has been assumed that it may be congeneric with male *Pennygullania*, another curious Lebanese neococcid.

**Material examined.** Larva, specimen number HAM-583 (Cocc-1321), Azar collection, housed provisionally in the Muséum National d'Histoire Naturelle, Paris. The larva, with dorsum exposed for some time became completely flattened and transparent, and reminds a slide mount. Secondary cracks made the right body margin difficult to see. Despite all these artifacts, many structures are accessible for accurate examination.

**Type locality and horizon.** Lower Cretaceous, Mdeyrij/Hammana, Caza Baabda, Mouhafazet Jabal Loubnan (Central Lebanon).

**Description.** Body flat, almost parallelsided, with deep anal cleft and protruding anal lobes, 630  $\mu\text{m}$  long, 380  $\mu\text{m}$  wide. Antennae inserted on frontal margin, ventrally, with considerable distance between them; six-segmented, the long first flagellar segment with an incision which means that in other specimens it may be divided, then the antenna would be 7-segmented, 300  $\mu\text{m}$  long; all joints strongly sclerotized, cylindrical, except apical one which tapers toward acute tip. Length of joints in  $\mu\text{m}$ : scape 35, pedicel 55, f1 72, f2 and f3 30 each, f4 78, the longest. On scape, setae not recognized, on pedicel a few short setae at apex, on first flagellar joint 4 setae near the incision and 5 setae at apex, one very long; on second and third flagellar joints one antennal bristle and 3-4 "other" setae (supposedly hair-like setae), on each; apical segment with 3 antennal bristles, 2 long setae (one on very tip), about 10 "other" setae and minute structures that may be coeloconic pegs. Clypeolabrum of the usual neococcid shape, about 100  $\mu\text{m}$  long, 60  $\mu\text{m}$  wide, with a pair of setae; labrum hidden. Labium conical, acute, 3-segmented, of pseudococcid-eriococcid type, with at least 5 pairs of setae, but the characteristic pseudococcid-putoid subapical setae (four pairs) not noted. Piercing stylets slightly protrude from the apex of labium, but the length of the loop can not be evaluated.

Legs slender with narrow coxae (neococcid feature), tarsus longer than tibia, all joints, including coxa, with numerous long setae, about 380  $\mu\text{m}$  long. Trochanter and femur separated, about 115  $\mu\text{m}$  long; trochanter with a very long (about as long as tibia) apical seta and 2-3 accessory setae; femur with at least 10 setae. Tibia about 85  $\mu\text{m}$  long, with about 10 setae, those on interior margin much lon-

ger than width of segment. Tarsus (with claw) 90-110  $\mu\text{m}$  long, with 14-18 setae, those on interior margin twice the segment width, tarsal digitules acute. Claw large, slender, slightly bent, about 30  $\mu\text{m}$  long, with a pair of very long knobbed digitules, without denticles.

Body end produced into a pair of strongly sclerotized, rounded anal lobes, with 5-7 strong (but not spine-like) setae at apex, dorsally. It could not be ascertained whether the anal cleft is deep, reaching the anal ring or shallow. A pair of very long (240  $\mu\text{m}$ ) apical setae is inserted ventrally in half way between anal ring and posterior margin of anal plates. Subapical setae, 1/4 the length of apical setae, are inserted close to apical setae, proximally. Two pairs of much shorter setae correspond with the fringe setae in Coccidae. Anal ring, with 6 setae ca 90  $\mu\text{m}$  long and wax secreting pores (secretion well preserved) inserted ventrally. Spiracles, circuli and ostioles not noted. Body margin with moderate sized hair-like setae (sometimes difficult to distinguish from fissures of amber). Submarginal and a few sternal setae observed on various segments. Small dorsal setae noted elsewhere. All dorsum with minute spirals, characteristic secretions of tri- and multilocular pores, but pores have not been identified, except perhaps a few on anal lobes.

**Note.** This specimen has been assigned in neococcids because it has a neococcid anal ring, sclerotized anal lobes with anal cleft, labium inserted between anterior coxae (much behind them in archeococcids) and slender coxae. The very long caudal setae suggest that it may be a crawler, but the large size and numerous setae on legs indicate that it may be rather a larva of an older stage. In general, it resembles a mealybug, and even the peculiar structure of the anal region could be considered an aberrant pseudococcid characteristics; similar lobes occur in *Chavesia* Balachowsky 1957, Rhizoecinae Williams 1969, as described by Beardsley (1970); however, it lacks the characteristic pseudococcid labial subapical setae (4 pairs) found in all species studied thus far (Koteja 1974a), but evidently lacking in larva *Pennygullania*. Also, assuming that this juvenile specimen is congeneric or at least closely related with the male *Pennygullania*, this group cannot be included in the Pseudococcidae or Putoidae (see note above), and supposedly represents an extinct family of the pseudococcid lineage.

## DISCUSSION

### General

There is a marked increase of the Cretaceous coccid fossils since the last communication (Koteja 1999a; state for 1997); it concerns especially the scale insects in the Lower Cretaceous amber from south-western France (Perrichot pers. comm.), and Alava, Spain (Arillo pers. comm.), previously not known; new abundant material in the Middle Cretaceous amber from Myanmar (Burma) (Koteja 2004, Rasnitsyn & Ross 2000, Grimaldi pers. comm.) and further valuable inclusions of Upper Cretaceous New Jersey amber (Grimaldi pers. comm.). Meanwhile, a Lower Cretaceous

impression from southern England (Koteja 1999b) and an inclusion in the Lower Cretaceous (Albian) Alaskan amber were published (Koteja & Poinar 2001). Now the results of the study on Lower Cretaceous Lebanese amber scale insects are presented. However, only about half of the available material has been examined and described.

Extensive search for new outcrops of Lebanese amber is being carried out by the junior author and his team in Lebanon and by Dr W. Weitschat and his coworkers in Jordan (pers. comm.), and further inclusion bearing material is permanently gathered. Also, Lebanese coccid inclusions are known to occur (or may occur being not recognized) in various collections, but are not accessible for study, thus the present paper is thought as the first contribution to the knowledge of fossil scale insects in the Lower Cretaceous Middle East amber.

The amber from Mdeyrij/Hammana in central Lebanon and from Jezzine (only one specimen studied) comes from Barremian-lowermost Aptian, ca 125 million years old. The slightly earlier finds of fossil coccids (impressions of Matsucoccidae and Xylococcidae) come from Berriasian-Valanginian in Siberia and Hauterivian in southern England (Koteja 1999b), and the younger, so far studied, from Albian on Alaska (97-104 myr) (Koteja & Poinar 2001), Turonian in New Jersey (90-94 myr) (Grimaldi et al. 2000) and Campanian in Canada (70-80 myr) (Beardsley 1969, Poinar 1992).

Araucarian or cheirolepidian resin is believed to have produced the Lebanese amber. The composition of taxa in Baltic amber (Koteja 1984) and the very sparse impression fossils indicate that the coccid inclusions may consist of species that lived on the resin exuding trees, in our instance, on some *Agathis*-like araucarian (for discussion see Azar 2000, Borkent 2000). The Araucariaceae are supposed to produce also other Cretaceous resin, except New Jersey amber that originated from Pinaceae and/or Taxodiaceae (Grimaldi et al. 2000). However, the question of the origin of various Cretaceous ambers is far from being solved.

The crust of the Lebanese amber pieces is ingrown with hyphae of fungi or some other organisms. The hyphae, of two types, can be seen even at low magnification. We are not aware of any study of this phenomenon.

Despite its age, the inclusions are well preserved, but almost completely impregnated with resin while being immersed, i.e., they appear transparent except some body parts in a few specimens. In this respect they correspond with the Canadian, Alaskan, Burmese and Dominican amber, and some pieces of New Jersey amber inclusions, being definitely different from the Baltic, Bitterfeld and most inclusions in New Jersey amber. This may result from the different type of resin or conditions of entombing (temperature) or both. On the other hand, the Lebanese inclusions are not coated (or rarely) with milky resin or crowds of larger bubbles of putrefaction gas, so characteristic of the Baltic and especially New Jersey amber inclusions (consult illustrations in Koteja 2000b). However, experiments (now general practice) with "clarifying" amber under high

temperature and pressure for jewellery purposes, may indicate that the “transparency” of the inclusions in the above ambers appeared as a result of fossilization in such conditions; this suggestion may be true at least with respect to the Canadian amber.

In addition to coccid inclusions, the pieces under study contain stellate hairs, fungus hyphae, remnants of other plants and arthropods, two specimens of Acarina, one lepidopteran and six Diptera (a few other dipterans have been earlier isolated). Of particular interest are the mites, obviously representing instances of phoresy. Phoretic mites associated with coccid males have also been found in Taymyrian and New Jersey amber, but none in the abundant Baltic amber; however, evident parasites have been noted on a matsuccid female in this last amber (for references see Koteja 1998, 2000a).

From the morphological point of view, the Lebanese amber coccids are well defined scale insects bearing features of the Upper Cretaceous, Eocene and Recent forms, although sometimes peculiar. The tails in *Palaeosteingelia* (2-4 pairs) are different from those in New Jersey amber and Recent *Steingelia*, but may be similar to those in the Alaskan *Kukaspis*. Peculiar are the paired tail setae inserted on two abdominal segments in *Pennygullania*, feature characteristic also of the Recent Phenacoccinae, but they are much stronger in the former. The proportion of forms with a circle of simple eyes is greater than in the extant forms. Unique seem to be the two circles of simple eyes in *Palaeotupo*, but this is ‘logical’ in the process of reduction of compound eyes. Especially peculiar is *Lebanococcus* with shortened antennae and telescopic abdomen; both features occur in Recent forms, but in none of evident archeococcids. Unusual are also the larvae; one JS-95, BM-53 (Cocc-1324) included “on belief” in *?Cretorthezia*, and another one HAM -475 (Cocc-1354) in *Pennygullania*. It seems to be reasonable to wait with further discussion and conclusions as to their status until more material has been gathered.

When this study was conducted, more than 1350 insect inclusions have been found in amber from the Hammana outcrops. The 34 coccid inclusions (the additional specimen recently found has not been included in the present study) constitute thus about 2.5 % of the collection; i. e., less than in New Jersey amber (10 %, compared with 13 % of all hemipterans), but more than in any other ambers, in which the proportion of scale insects does not reach 1 %. The proportion of coccids in amber from the Jezzine outcrops (A. Acra collection) cannot be evaluated because the total number of specimens is unknown, and because we do not know whether the single available specimen represent all coccid inclusions in this collection. Nothing is known about the number and proportion of scale insects in other Lebanese amber collections.

Considering frequency of taxa, the Lebanese coccid fauna is dominated by one group, the Steingeliidae, which constitute 54 % of the sample, and several amber pieces bear more than one inclusion of this group. Three groups

are represented by 2-3 specimens, and the remaining groups by one inclusion only. Similar proportions occur in other fossil resins already examined: Grimaldiellidae in the New Jersey amber, Inkaidae in Taymyrian amber, Matsuccidae in Baltic and Bitterfeld amber, which constitute about 60 % or more of the respective faunas. Unfortunately, comparable data are lacking for the recent fauna.

Within the Sternorrhyncha, the taxonomy of recent and fossil Psyllinea is based on adult (alate) forms of both sexes, the larvae (nymphs) being poorly known (Loginova 1964). In the Aleyrodinea, the taxonomy of recent forms is based on the last preadult instar, the so called “puparium”, but that of the fossil forms, on winged adults (Shcherbakov 2000). In the polymorphic Aphidinea the taxonomy of recent forms bases mainly on parthenogenetic winged females, and that of the fossil forms on both “alate” and “apterous” forms without special distinction of instar (juvenile or adult) and sex (Heie 1967, 1999; Węgierek 2000). Obviously, with respect to impression fossils most important are the wings and their venation.

In the extremely dimorphic scale insects, recent forms are classified basing on adult (apterous) females, with very few exceptions in the archeococcids (e. g., *Neomargardes erythrocephala* Green 1914 established on adult alate male); however, attempts have been made to form classificatory systems based on juvenile instars in groups where adult ovipositing females are not suitable for microscopic examination, e. g., in the Kermesidae (Bear & Kosztarab 1987). With respect to the sparse coccid fossils we have to rely on what is available, with special concern of taxa at family level (for discussion see Koteja 2000a, b). As a result, some taxa are based on adult females (Ortheziidae), some on crawlers (Eriococcidae, Kermesidae) and most on alate and apterous males. However, with the increasing number of fossils available for study, also the chance of meeting various instars and sexes of the same species entombed in the same amber piece also increases (Koteja 2000a, Tab. 3).

In the recently studied New Jersey amber scale insects (Koteja 2000b), two genera have been established on larvae, i. e., *Keithia* (Eriococcidae) and *Labiococcus* (Labiococcidae related to Putoidae), the remaining ones on males. Eriococcid males were not represented in this amber, and *Labiococcus* was considered relative (congeneric or even conspecific) of *Solicoccus* (male). In the Lebanese amber, all taxa have been based on alate males, and the larval specimens have been ascribed to respective genera “on belief” since there was no evidence of their congeneric (even con-familial) affiliation.

## CRETACEOUS SCALE INSECTS

The occurrence of various coccid groups in Cretaceous is presented in table 3. The groups, considered to be equivalent to families, have been divided into two superfamilies, the Orthezioidea or archeococcids and Coccoidea or neococcids, as they are understood in the recent fauna (Koteja 2001 and references cited therein). The archeococ-

Family	L. Cret.	U. Cret.	Eocene	Recent
Orthezioidae				
1. Ortheziidae	+	*	+	+
2. Matsucoccidae	+	+	+	+
3. Xylococcidae	+	*	*	+
4. Margarodidae	-	-	+	+
5. Coelostomidiidae s.l.	*	*	+	+
6. <i>Jersicoccidae</i>	-	+	-	-
7. <i>Hammanococcidae</i>	+	-	-	-
8. Monophlebidae s.l.	*	*	+	+
9. <i>Lebanococcidae</i>	+	-	-	-
10. <i>Grimaldiellidae</i>	-	+	-	-
11. Steingeliidae	+	+	*	+
12. <i>Kukaspidae</i>	-	+	-	-
13. Pityococcidae	*	*	+	+
14. <i>Electrococcidae</i>	+	+	-	-
Coccoidea				
1. Putoidae s.l.	+	*	+	+
2. <i>Labiococcidae</i>	-	+	-	-
3. Pseudococcidae s.l.	*	*	+	+
4. <i>Pennygullaniidae</i>	+	-	-	-
5. Eriococcidae s.l.	-	+	+	+
6. <i>Inkaidae</i>	-	-	+	-
7. Kermesidae	-	-	+	+
8. Coccidae s.l.	-	-	+	+
9. Diaspididae	-	-	+	+

Table 3. Occurrence of scale insect groups in Cretaceous and Cenozoic + = present, - = absent, \* = postulated occurrence not evidenced by fossils. Extinct groups in italics and with a space at left margin

cid families have been arranged (grouped) on the following criteria accessible in fossils:

1. Devices joining wings in flight: (a) narrow fold for reception hamuli as in aphids or (b) a pocket on protruding lobe. The former occurs in families 1-3, latter in the remaining groups. The joining devices can be entirely reduced, e. g., in some Ortheziidae (Koteja 1986), and the hamuli can be substituted functionally with hooked apex of halteres in Margarodidae s. str.

2. Structure of scutum and scutellum: (a) scutum solid, scutellum rectangular, pentagonal or oval (if triangular, then with one angle directed caudad), (b) scutum solid or with membranous areas of various size and shape, scutellum triangular, with one angle directed headward, (c) scutum with membranous areas, scutellum tubular. State (a) occurs in families 1-3, state (b) in families 4-10, state (c) in families 11-14.

3. Eyes: (a) compound eyes (b) circle of unicorneal eyes, (c) two pairs of simple eyes. State (a) occurs in families 1-9, state (b) in families 10-14, state (c) does not occur in archeococcids, provided that *Pennygullania* has correctly been placed in neococcids.

4. Tail devices: (a) unpaired waxy tail on one or two abdominal segments, (b) paired lateral setae associated, or not, with wax secretions on one or several abdominal seg-

ments, (c) projections of abdominal pleurites on one or more abdominal segments ("fleshy tassels", Morrison 1928), (c) no tail organs, sometimes substituted with elongated abdomen and/or penial sheath. State (a) occurs in families 1-7, state (b) in families 11-14, state (c) in the Monophlebidae, state (d) in families 9-10 and some Coelostomidiidae.

5. Costal wing margin: (a) well developed subcostal ridge with pterostigma, (b) well developed subcostal ridge without traces of pterostigma, (c) well developed pterostigma with much reduced subcostal ridge. State (a) occurs in Jersicoccidae, Grimaldiellidae and Lebanococcidae, state (b) in families 1-3, 5, 8, 11-14, state (c) in the Margarodidae s. str.; conditions in Hammanococcidae are not known. In the Recent fauna, a well developed pterostigma has been noted only in Margarodidae s. str.

6. Microtrichia: Generally are absent in archeococcids, noted in Grimaldiellidae and Electrococcidae, and also in the Recent Phenacoleachiidae, not found among fossils.

7. Antennal setae: (a) much longer than segment width and arranged in whorls, (b) about as long as segment width and scattered. State (a) occurs in Jersicoccidae, Hammanococcidae and Monophlebidae (families 6-8), state (b) in remaining groups.

Well defined Ortheziidae were found in Lebanese and Baltic amber (as far, not recorded from Upper Cretaceous). Recent investigations revealed an abundant and diverse ortheziid fauna on the bottom of tropical forests (Kozár & Miller 2000, Kozár & Koneczná-Benedicty 2000).

The Matsucoccidae, with their characteristic pinnate wing sculpture, have been first described from Baltic amber, then found in the extant fauna (Holarctic) (for discussion see Koteja 2000b). Well preserved impressions are known from Lower Cretaceous, inclusions from Upper Cretaceous New Jersey amber, being the dominant group in Baltic and Bitterfeld amber, and constituting about half of known coccid fossils (for review see Koteja 2000a, b). Their structure has little changed from Cretaceous to the present and they might have adopted to Pinaceae in Upper Cretaceous. Morrison (1928) and Beardsley (1968) suggested that they might be the most primitive scale insects.

An impression believed to be related to the Xylococcidae was found in Siberian Lower Cretaceous deposits together with the above matsucoccid impressions (Koteja 1989a). They have not been noted in Upper Cretaceous, and the abundant Baltic amber has not been thoroughly examined yet. In the Recent fauna they are represented by a few species in Holarctic and Neotropic.

In the system of Morrison (1928), the Matsucoccidae and Xylococcidae are placed close each other, the males also are similar, but Gullan & Sjaarda (2001) placed them on quite distant branches of their cladogram.

The Margarodidae s. str. (ground pearls), of worldwide distribution, are peculiar in many aspects, being distinct from all other Recent coccids by the fossorial forelegs, well developed pterostigma and structure of haltere. Forms with well developed pterostigma are quite common in Baltic amber (cf. Weitschat & Wichard 1999), but have not

been found in Cretaceous. It is unlikely that the Margarodidae may have anything in common with the Cretaceous Jersicoccidae and Grimaldiellidae in which the wing and pterostigma have a quite different structure.

The traditional Coelostomidiidae appear to be an artificial unit (Gullan & Sjaarda 2001) comprising also forms similar to the Margarodidae and Monophlebidae; consequently, their status among fossils is also obscure.

The Monophlebidae are well defined by the fleshy tassels, long antennal setae arranged in whorls and an eversible endophalus. Such forms have first, and only, been found in Baltic amber (Koteja 1998). Among the Cretaceous groups, the Hammanococcidae from Lebanese amber and the Jersicoccidae from New Jersey amber have long antennal setae arranged in whorls, but also a tail tuft, not found in the abundant and diverse Recent Monophlebidae. Both Jersicoccidae and Hammanococcidae seem to be extinct groups.

The Lower Cretaceous Lebanococcidae, apparently extinct, with shortened antennae and peculiar abdomen may be aberrant members of either the margarodid or monophlebid lineage.

The Upper Cretaceous Grimaldiellidae are peculiar with respect to the structure of wing (well developed subcostal ridge combined with pterostigma, presence of microtrichia), disintegrated compound eyes (there is a circle of single ommatidia), lack of any tail devices and presence of an eversible endophalus; in addition, they were very abundant (Koteja 2000b). Unfortunately, nothing is known about the female, feeding behaviour and life history, and no other, even slightly similar, forms have been found in the Cretaceous or Baltic amber. However, the presence of a distinct triangular scutellum indicates that their placement within the margarodid-monophlebid grouping is correct.

The affiliation of the Steingeliidae with the archeococids is very well documented by the morphology of the female and life history (Morrison 1928, Koteja & Žak-Ogaza 1981). Their position was questioned since the discovery of the male, extremely different from any archeococids (Theron 1958). In the cladogram by Gullan & Sjaarda (2001) based on adult female and crawler, the Steingeliidae appear as a sister group of all other archeococids except Ortheziidae. This would be in accord with the opinion based on the male and is supported by the paleontological record. Recent Steingeliidae are represented by *Steingelia gorodetskia* in the Palearctic and *Stomacoccus platani* known only from the type locality in Nearctic. In Baltic amber, evident steingeliids have not been found thus far, but an inclusion in the New Jersey amber (Upper Cretaceous) has been placed in *Steingelia* which suggests a great morphological stability at generic level. Numerous steingeliid inclusions have been found in Lower Cretaceous Lebanese amber (present study), but being distinct from the recent forms by the shape of wings and structure and number of tails. The tails seem to be similar to the Middle Cretaceous Kukaspidae from Alaskan amber (Koteja &

Poinar 2001), but the penial sheath is definitely different in these groups.

Females of the Recent Pityococcidae (Nearctic) are superficially similar to those of the Matsucoccidae, and live on the same host, but bear mouthparts. McKenzie (1942), who discovered these peculiar archeococids, affiliated them with the Coelostomidiidae. Koteja (1988) described a minute apterous male, *Cancerococcus apterus*, and placed it among the eriococids. Miller & Gimpel (1999) transferred it to the Pityococcidae. Between 1988 and 1999 a number of fossils were found in Baltic and Bitterfeld amber, including male+female syninclusions (Koteja 1999a) which confirmed the correct placement of these fossils in the Pityococcidae. Much earlier, Beardsley (1969) described a fossil, *Electrococcus canadensis*, from Upper Cretaceous Canadian amber and suggested its relation to the Pityococcidae, but did not place it formally to this family. Koteja (2000b) found similar forms (*Turonicoccus*) in New Jersey amber and established the family Electrococcidae. Members of this group have been found also in the Middle Cretaceous Burmese amber (Koteja 2004) and in the Lower Cretaceous Lebanese amber (present study). Electrococcidae bear wing microtrichia, *Cancerococcus* is wingless, and the conditions in Recent Pityococcidae are unknown. In any case, this most specialized (considering males) archeococid group (Pityococcidae+Electrococcidae) originated before, or at the beginning of, Cretaceous and survived successfully to the present.

The Putoidae have been established by Beardsley already in 1969, but their status has been under permanent dispute until now, and most students place the genus *Puto* in the family Pseudococcidae (cf. Ben-Dov 1994). In Baltic amber, the Putoidae are very distinct and quite numerous, represented by various forms, and supposedly have first been described as "*Monophlebus trivenosus*" by Germar & Berendt (1856). Another suggested member of this group has been found in New Jersey amber, but placed in a distinct genus, *Solicoccus*, because of two pairs tail rods (Koteja 2000b). In the same amber, larvae similar to putoids, but with very long labium, *Labiococcus*, have been found, and, basing on both larvae and male, the family Labiococcidae has been erected. In Lebanese amber, a putoid-like male with one pair of tail rods, but with two rows of simple eyes, has been discovered and placed formally in the Putoidae (present study).

*Pennygullania* from Lebanese amber is the first and only Cretaceous male with two pairs of simple eyes (present study). Although bearing several peculiar features (some occurring in the Coccidae) it may be related to the mealybug (Putoidae+Pseudococcidae) lineage. This suggestion appears also from the characteristics of the larva.

First representatives of definite Eriococcidae have been found in Upper Cretaceous New Jersey amber (Koteja 2000b), and a group related to them, Inkaidae, in the Taymyrian amber (Koteja 1989). Undescribed eriococids occur also in Canadian amber. As far, this is all information about neococids in Cretaceous.

## CONCLUSIONS

The concept of the main radiation of scale insects presented by Balachowsky (1942), Borchsenius (1950) and Bodenheimer (1952) and adopted by their followers, and based exclusively on morphology, biology and distribution of the Recent fauna, as well as the application of the names “archeococcids” and “neococcids”, has been supported also by the fossil record.

The present study also supports the belief of the antiquity of scale insects. In Lower Cretaceous coccids were represented by all main branches and many peculiar specialized groups that became extinct during Mesozoic. It is also true, that the scale insects are a young group that evolved and radiated with the flowering plants (Hoy 1962 and followers), provided that this opinion refers to the neococcids.

It became clear that the discussion on the “primary” host of scale insects was nonsense; simply, coccids used those hosts which were accessible in given times; and the feeding behaviour might have changed many times. For instance, the extant Matsucoccidae live exclusively on pine, the same may be true for Eocene forms, but not for the Lower Cretaceous ones. Recent Xylococcidae live on conifers and various dicotyledonous trees which apparently were non-existing in Lower Cretaceous. *Steingelia* lives exclusively on birch, but this does not mean that it evolved with the origin of this host.

An important conclusion from the present study is that the basic structure and the morphological diversity (considering male), with special reference to the wings, of the Lower Cretaceous scale insects are comparable with those of the Recent coccids. This means that, searching for Mesozoic coccid ancestors, we must look for forms similar to extant scale insects, and not to aphids or other sternorrhynchans. This appears also from the structure (wings) of Triassic and Jurassic aphids which apparently are remains of aphids, and not of any “intermediate” forms. However, this also means that definite scale insects existed in Paleozoic.

The present study does not answer the question why fossils of “true” scale insects are so rare (practically non-existing) in pre-Cretaceous sediments. We believe that they exist, but are overlooked because of the poor wing “venation”. However, this is not the case with the monophlebids which have leathery or strongly sclerotized wings similar to some “auchenorrhynchans”.

Although the interpretation of various structures in fossils is uncertain, and the suggestions concerning relationships between juvenile instars and adults, male and female, as well as between taxa, may be misleading, erroneous or simply guesses. Paleontological investigations did provide some information on the history of scale insects, as far, back to the Lower Cretaceous. In any case, our imagination of the coccid fossils is somewhat more realistic than only some years ago (Koteja 1985) when based on a few Baltic amber inclusions.

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