

New fossil taxa of Monophlebidae (Sternorrhyncha: Coccoidea) from Baltic amber

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Abstract. The family Monophlebidae is distributed worldwide and is classified as one of the “archaeococcoid” families. After almost 160 years since Germar & Berendt (1856) described the first and so far only fossil monophlebid species, *Monophlebus irregularis*, two new fossil species of a new and undoubtedly monophlebid genus *Palaeophlebus* gen. n. are described from Baltic amber. Morphological features of the new genus and its two species, *P. hoffeinorum* sp. n. and *P. kotejai* sp. n., are discussed.

INTRODUCTION

Scale insects (Coccoidea) are representatives of the Sternorrhyncha, a monophyletic suborder of Hemiptera. This superfamily contains nearly 8000 species, belonging to 48 families (including extinct and extant taxa), but its family-classification is controversial. Coccoidea are very often divided into two major informal groups, the archaeococcoids and neococcoids, based on the presence or absence of characters interpreted as ancestral (Gullan & Martin, 2009).

The family name “Monophlebites” was first used by Signoret in 1875. Maskell (1880) raised this group to the family level, but Morrison (1928) treated the monophlebids as a subfamily Monophlebinae within the Margarodidae. Morrison considered that it comprised 5 tribes: Drosichini, Iceryini, Llaveiini, Monophlebini and Monophlebulini. Now all subfamilies and most of the tribes sensu Morrison (1928) have been given family status (Koteja, 1974; Foldi, 2005; Hodgson & Foldi, 2006; Gullan & Cook, 2007; Hodgson & Hardy, 2013).

The first scale insects in Baltic amber were described in the second half of the 19th century, and the first documented fossil representative of the Monophlebidae, *Monophlebus irregularis* Germar & Berendt, 1856 in Eocene Baltic amber, was described by Germar & Berendt (1856) and commented on by Koteja (1984). It has binodose antennal segments and caudal extensions on its abdomen. However, the type material, which was deposited in the Koenigsberg Collection, was lost during the Second World War (Bendov et al., 2014). General information on inclusions in Baltic amber, including those preliminarily identified as monophlebids (25 males, 3 females, 22 larvae, 5 crawlers), can be found in Koteja, 1998.

In the present study, the detailed descriptions of a new extinct genus, *Palaeophlebus* gen. n., clearly belonging to Monophlebidae, and two new species *Palaeophlebus kotejai* sp. n. and *P. hoffeinorum* sp. n., are presented.

MATERIAL AND METHODS

The nomenclature of body structures and wings follows Hodgson & Foldi (2006) and Koteja (2008), respectively. Drawings are naturalistic, which means they also include artifacts, deformations of the body, shriveling and the semi-parallel positions of the appendages. Body parts obscured by the milky resin are marked with sparse dots. As noticed by Koteja (1984), the dimensions of semi-parallel structures and the details are error-prone; moreover, amber itself acts as a lens. Thus, the likelihood that the measurements are not accurate should be considered. Measurements are approximate, antennae and legs may be deformed and optically shortened in the total figure. All measurements are given in micrometers (µm). Nikon MZ1500 and Nikon DS-FIZ stereoscopic microscopes, each equipped with a camera and changeable direct and transmitted lighting, were used for the microscopic examinations. Photographs were taken using Nikon DN 100 and Nikon Digital Sight DS-V3 cameras and the Lucia-Net and NIS-Elements D software.

SYSTEMATIC PALAEONTOLOGY

Order Hemiptera Linnaeus, 1758

Suborder Sternorrhyncha Duméril, 1806

Superfamily Coccoidea Fallén, 1814

Family Monophlebidae Signoret, 1875

Genus *Palaeophlebus* gen. n.

Type species. *Palaeophlebus hoffeinorum* sp. n., designated here.

Etymology. “*Palaeo*” (Latin) – ancient, “*phlebus*” – the same ending as in *Monophlebus* – the first genus described within the Monophlebidae.

Gender. Masculine.

Generic diagnosis. Large (2440–2730), body fairly setose with hair-like setae, hairs and collar setae, no signs of pores. Antennae long, 10-segmented, segments of flagellum irregularly nodose to slightly trinodose, with long setae not forming distinct whorls, as in recent representatives of Drosichini. Wings large, infusate, with first light line reaching posterior margin, second light line fading before

posterior wing margin. Margin of wing slightly indented where first light line ends. Abdomen with a pair of caudal extensions on abdominal segment VIII, each about 1/3 of abdomen length, with a few long setae on each apex. Penial sheath elongated and strongly sclerotized, bilobed at apex, extending past margins (between caudal appendages) of abdominal segment VIII.

Comment. For discussion of the relationship of *Palaeophlebus* with extant genera, see the final Discussion.

***Palaeophlebus hoffeinorum* sp. n.**

(Figs 1, 3A, C, E)

Etymology. Species name devoted to Mrs Christel Hoffeins and Mr Hans Werner Hoffeins, Hamburg, Germany, who collected these scale insects and kindly offered them for study.

Stratigraphic horizon. Eocene.

Type material. Holotype male: #1406-5, alate, from Baltic amber, large, 2730-long, width at mesothorax 1112, deposited in the Christel & Hans Werner Hoffeins collection, Hamburg, Germany. A piece of amber containing the inclusion was cut, ground, polished and embedded in epoxy resin. Syninclusions: stellate hairs. Scale insect inclusion well preserved, observable mainly from the ventral side. Large parts of the body, especially the dorsal part, coated with milky resin. Apical segment of the left antenna hidden beneath the mesothoracic tibia and the right antenna bent towards the dorsum and curled. Only the left wing observable, the right is folded and details of its morphology not accessible for study.

Paratype male. Cocc-1458, alate, from Baltic amber, large, 2580-long, deposited in the Jan Koteja collection, Department of Zoology, University of Silesia, Katowice, Poland, No. KOT-0748. Shape of amber piece irregular, 20×10×8 mm wide with nine layers, light yellow, polished. Syninclusions: stellate hairs, Diptera. Scale insect inclusion well preserved, but observable mainly from lateral view; dorsal part of body coated in milky resin, ventral part covered with air bubbles.

Species diagnosis. The following characters are distinctive for *Palaeophlebus hoffeinorum* sp. n.: compound eyes with 60–80 small ommatidia, segments of antennae beyond the second one irregularly nodose, with long setae not forming definite whorls, subcostal and cubital ridges almost equal in length; claws slightly bent.

Description

Head. Triangular in dorsal view, with large compound eyes. Length of head not observable when viewed dorsally, width across compound eyes 530. Dorsally: details of morphology not observable, covered by milky resin. Laterally: each compound eye about 240 long and 160 wide, with 60–80 ommatidia, each ommatidium 25–27 in diameter.

Each compound eye with a narrow, lightly sclerotized ocular sclerite along dorsal margin, each with a single ocellus dorsally, width of observable ocellus difficult to measure as surrounded by a small bubble. Ventrally with a strongly sclerotized series of ridges forming a five-armed star, composed of (i) ventral midcranial ridge anteriorly, (ii) a pair of lateral preocular ridges and (iii) a pair of preoral ridges posteriorly. Ventral part of epicranium mainly membranous, except for some light sclerotization at point where ventral midcranial ridge, preocular ridges and preoral ridges meet, and also covering most of the area adja-

cent to the preoral ridges. Membranous parts of epicranium covered with numerous setae, probably hair-like and hairs.

Antennae. 10-segmented; longer than body length; total length about 2870 (ratio of the total body length to antennal length 1 : 1.05). Scape 150 long, 100 wide, sclerotized, with a basal articular process extending posteriorly from each scape; with several hair-like setae, longest seta about 138; bifurcated setae absent. Pedicel 160–180 long, about 85 wide, with ca. 16 long setae, longest 130. Segments III–X of flagellum irregularly nodose, width of all segments similar, long setae not forming regular whorls. Flagellar segments each with hair-like setae, fleshy setae, antennal bristles and hairs, longest setae exceeding 2–3× segment width. Length of segments: III 360–400, IV 305, V 314, VI 300, VII 344–360, VIII 260–340, IX 320, X 360.

Thorax. Prothorax. Laterally with strong cervical sclerites; pleural ridge present, extending dorsally, connected posteriorly with pleural ridges.

Mesothorax. Laterally: prealare elongate and narrow; mesepisternum heavily sclerotized, with a strong subepisternal ridge; mesopleural ridge well developed; mesothoracic spiracles indistinct; mesepisternite small, slightly sclerotized.

Metathorax. Laterally: metepisternum unsclerotized; metapleural ridge weakly sclerotized; metapleural wing process heavily sclerotized; metathoracic spiracles not observable; metepimeron slightly sclerotized.

Wings. Fore wings large and well developed; 2840–3310 long, 1210–1550 wide (ratio of total body length to forewing length: 0.9 : 1 for holotype; 0.82 : 1 for paratype). Wing membrane with the microsculpture characteristic of monophlebid. Base of wing membrane broad, but proximal hind margin with alar lobe not well visible. Subcostal ridge well defined, but truncated before wing apex, extending to 2/3 of total wing length. Cubital ridge strong and bent upward, approximately equal in length to subcostal ridge, oriented upward terminally. Both light lines present, anterior line long, running straight and reaching posterior wing margin, where wing margin slightly indented. Posterior light line distinct but short, fading and not reaching wing margin. Hamulohalteres sclerotized, quite narrow, each 240 long, 67 wide, with 3 hamuli, each hooked.

Legs. Slender; mesothoracic legs possibly longest. Length of coxae: I 190, II 280, III 210, each with many hair-like setae. Length of trochanter + femur: I 820, II 870, III 840; trochanter elongated, with several short, slender setae and a single very long flagellate seta on distal ventral part; femur with many setae, mostly short with some on ventral surfaces longer; bifurcated setae not observed. Length of tibia: I 850, II 900, III 830, each with short bifurcated setae along almost whole length of ventral and lateral margins; many long flagellate, together with a few bifurcated setae along dorsal margin (those on dorsal margin bifurcated and longer than those on ventral and lateral margins); with 2, tibial spurs on distal apex. Tarsi 2-segmented, proximal segment very short and triangular, combined length of both tarsal segments: I 380, II 370, III 350; bifurcated setae present along ventral margins and also with a few on dorsal

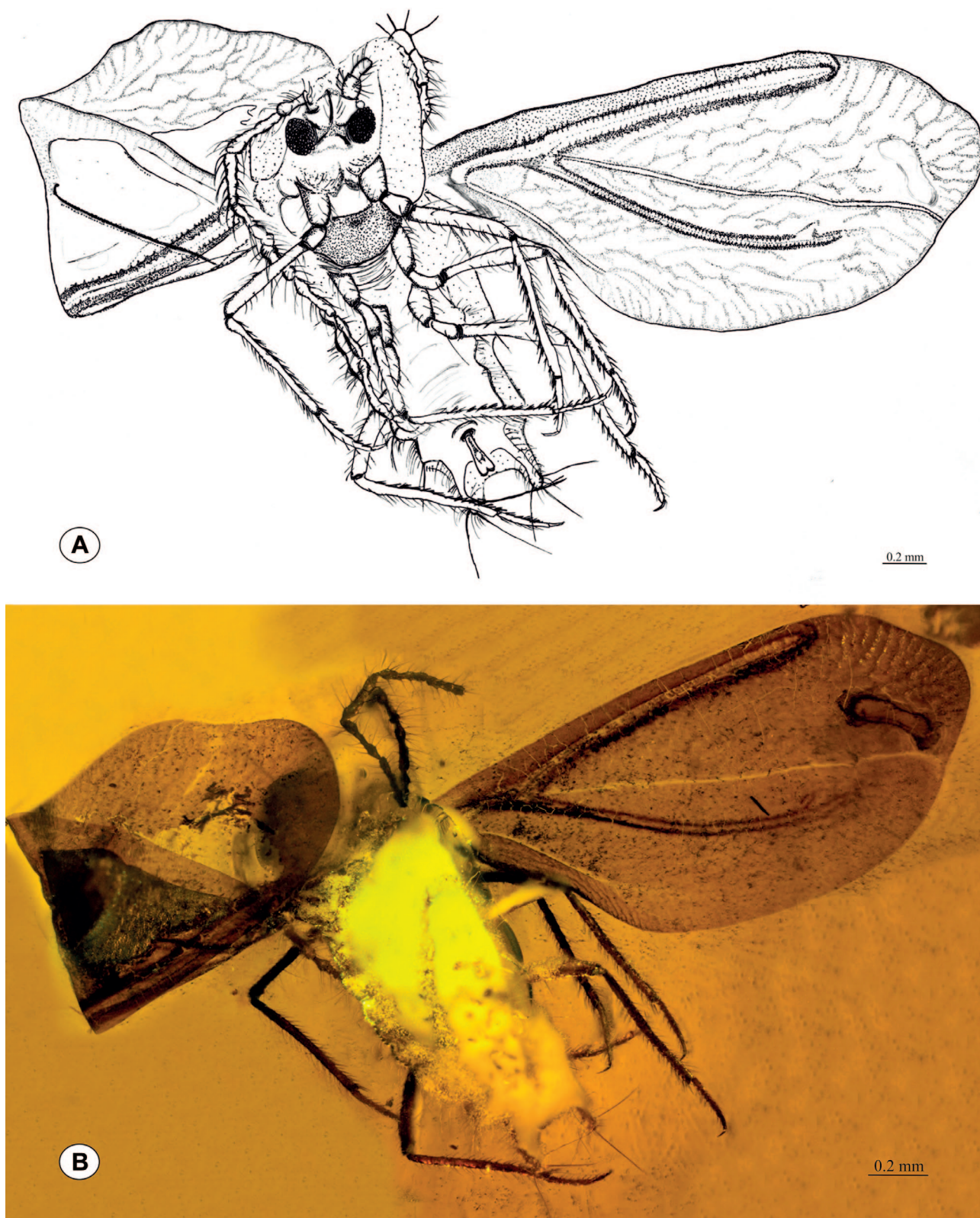


Fig. 1. *Palaeophlebus hoffeinorum* sp. n. (holotype, #1406-5). A – drawing, ventral side; B – photomicrograph, dorsal side.

margins. Tarsal digitules represented by two fine, short setae on dorsal margin. Claws slightly bent, elongated and slender, length: I 90 II 80, III 70, without denticles, but with short setose digitules near bases of the claws.

Abdomen. Caudal extensions present only on segment VIII, each about 320 long; but with margins of penultimate

and ante-penultimate segments strongly protruding. Dorsally details of morphology not visible due to a covering of milky resin. Ventrally: abdominal setae forming narrow bands on segments V–VIII. Sternites very narrow, situated at segmental boundaries. Laterally: pleural setae not divided into dorsal and ventral-pleural groups. Caudal exten-

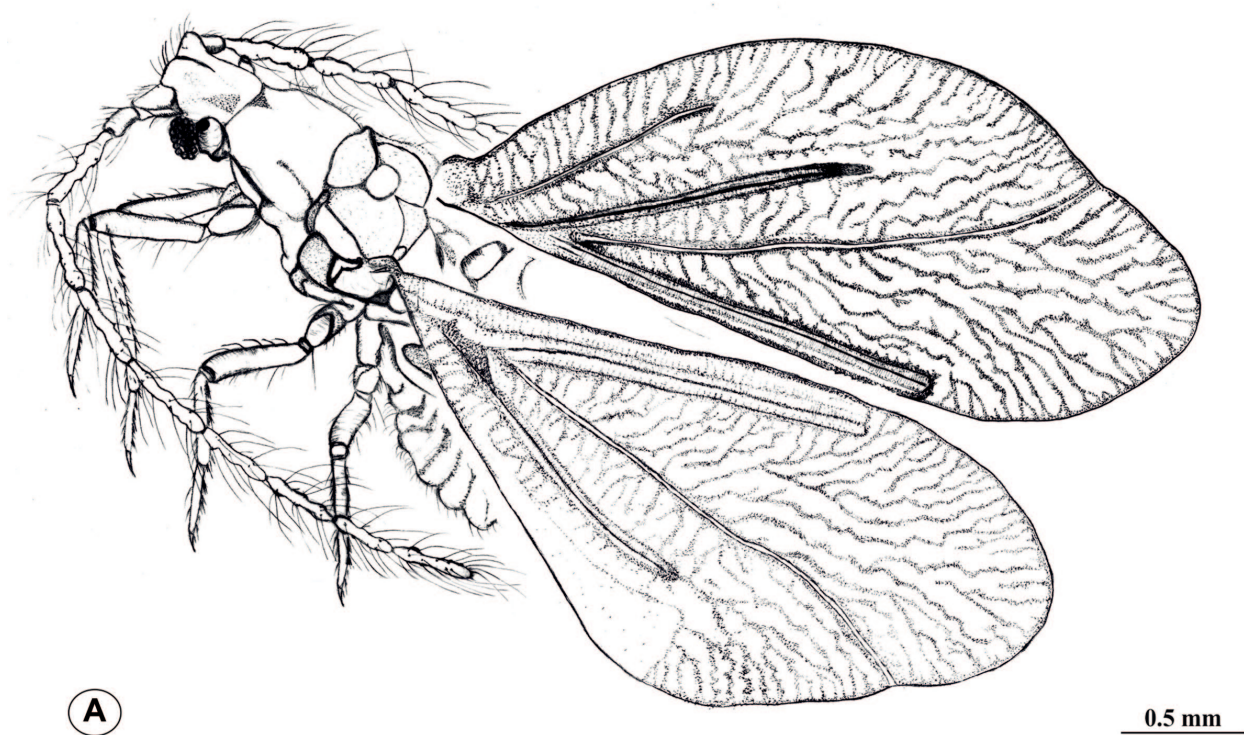


Fig. 2. *Palaeophlebus kotejai* sp. n. (holotype, Cocc-0117). A – drawing, dorsal side; B – photomicrograph, ventral side.

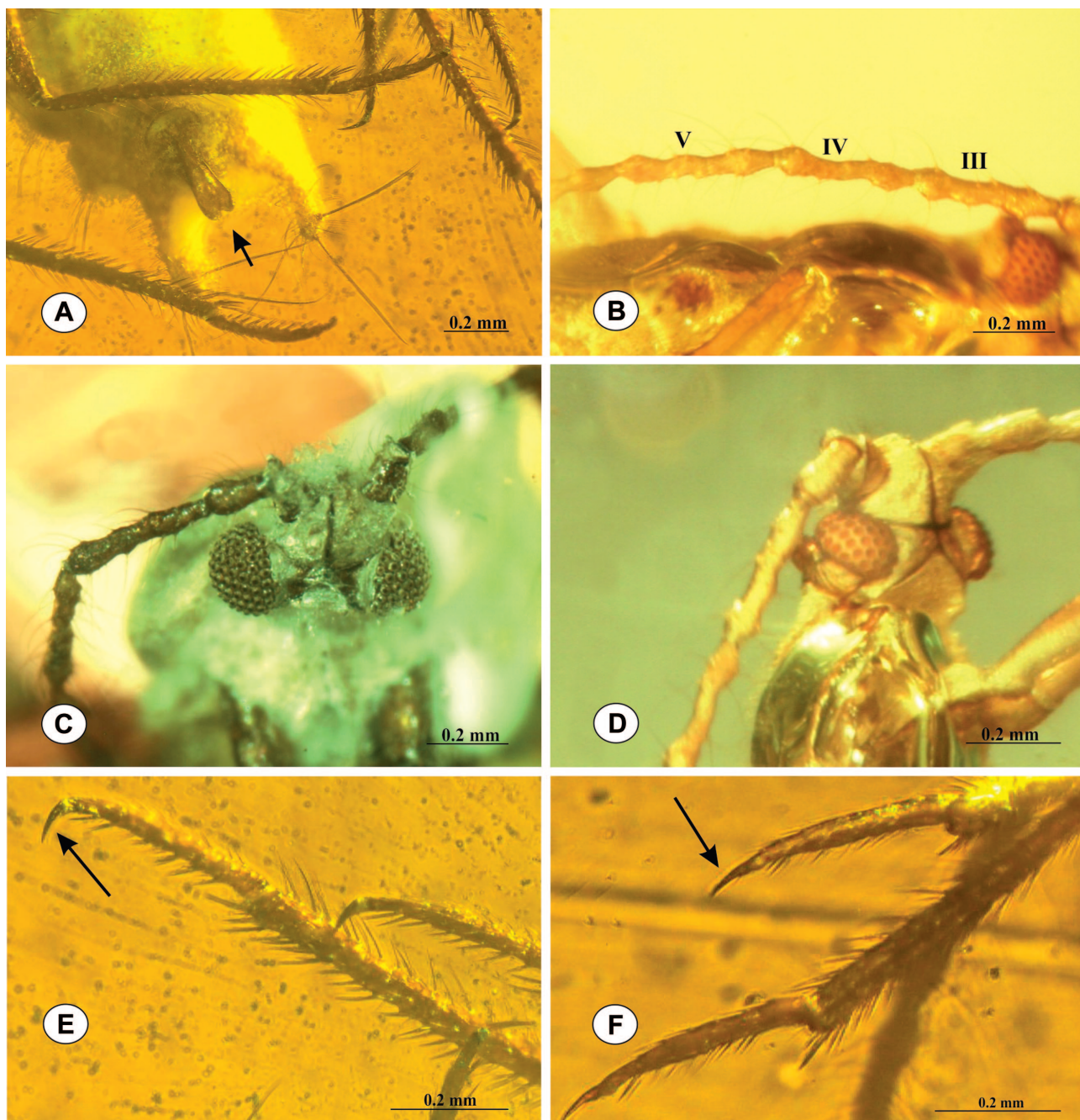


Fig. 3. Photomicrographs of new species. A, C, E – *Palaeophlebus hoffeinorum* (holotype, #1406-5); B, D, F – *Palaeophlebus kotejai* (holotype, Cocc-0117). A – penial sheath; B – irregularly trinodose structure of antennal segments; C, D – head, ventral view; E, F – claws.

sions on segment VIII each with 3 very long setae, each up to 400–510 long. One spiracle observed dorso-laterally on anterior margin of segment VII.

Genital segment. Anus located between caudal extensions on segment VIII, surrounded by an oval sclerotized ring (58 diameter); setae and pores not observed. Penial sheath heavily sclerotized, about 280 long, 92 broad at apex, extending beyond margins of abdominal segment VIII, but not longer than caudal appendages; broadening apically with apex clearly bilobed. Aedeagus heavily sclerotized, lying in a groove along ventral margin of penial sheath, with a bifid apex. Eversible endophallus not observed.

Palaeophlebus kotejai sp. n.

(Figs 2, 3B, D, F)

Etymology. This species is named in honour of the late Professor Jan Koteja, who was one of the best specialists on fossil scale insects.

Stratigraphic horizon. Eocene.

Type material. Holotype male: Cocc-0117, alate, from Baltic amber, large, 2440-long, deposited in the Jan Koteja collection, Department of Zoology, University of Silesia, Katowice, Poland, No. KOT-0855. Shape of amber piece irregular; 20×20×10 mm wide, with ten layers; colour: yellow and transparent, polished. Syninclusions: stellate hairs, Diptera, Formicidae, Colembolla, Acarina. Condition of scale insect inclusion: details of morphol-

ogy very well preserved, visible from dorsal and lateral side, but right side and part of venter part of thorax and abdomen covered by a big bubble.

Paratype male. Cocc-1457, alate, from Baltic amber, body length not observable; width of mesothorax 4500, deposited in the Jan Koteja collection, Department of Zoology, University of Silesia, Katowice, Poland, No. KOT-747b. Shape of amber piece subrectangular, 12×7×3 mm wide with three layers, light yellow and transparent, polished. Syninclusions: none. Condition of scale insect inclusion: well preserved, observable mainly from dorsal side; right wing slightly folded; ventral side hidden by bubble and milky resin. Legs, wings, antennae and details of the dorsal part of thorax all clearly visible.

Other material examined. Cocc-1449, alate male from Baltic amber, deposited in the Jan Koteja collection, Department of Zoology, University of Silesia, Katowice, Poland, No. KOT-0739. Shape of amber piece irregular, 30×25×15 mm wide with nine layers, yellow and transparent, polished. Syninclusions: stellate hairs, Acarina, Aphidomorpha, Diptera. Condition of scale insect inclusion: poorly preserved, body covered with milky resin, but from ventral view left wing, part of right antennae, with segments VI–X, tibia and tarsus of anterior pair of legs visible.

Note. Description mainly based on holotype specimen.

Species diagnosis. The following characters are distinctive for *P. kotejai* sp. n.: compound eyes with 40–60 ommatidia; flagellar antennal segments more or less distinctly trinodose, with long setae tending to cluster in three groups, but do not form distinct whorls as in recent representatives of many Monophlebidae; cubital ridge shorter than subcostal ridge; claws straight.

Description

Head. Typical for monophlebid, with a triangular extension between bases of antennae. Length 380, width across compound eyes 370. Dorsally: postoccipital suture well developed, with a triangular postocciput posteriorly. Dorsomedial part of the epicranium membranous; midcranial ridge absent. Laterally: each compound eye ca. 170 long, 160 wide, with 40–60 ommatidia, each ommatidium 25 wide; with a broad ocular sclerite; with a single ocellus situated dorsad to each compound eye; width of each ocellus 35; each ocular sclerite with a longitudinal postocular ridge. Ventrally with a strongly sclerotized series of ridges forming a five-armed cross, composed of (i) ventral midcranial ridge anteriorly, fusing with (ii) a pair of preocular ridges, which originate between each antenna and a compound eye, and (iii) a pair of preoral ridges posteriorly. Rest of ventral part of epicranium membranous, except for a lightly sclerotized area close to margins of preocular and preoral ridges. Ocular sclerites ventrally quite large and apparently swollen.

Antennae. 10-segmented, longer than body; total length about 2900. Scape 170 long, 11 wide, with short setae and a basal articular process extending postero-laterally from each scape. Pedicel 120–150 long, 74 wide, with a few short and one long seta. Segments III–IX of flagellum irregularly trinodose but of similar width; each segment with long setae tending to form 3 whorls; each segment with hair-like setae, fleshy setae, antennal bristles and hairs; longest setae exceeding 2–3× segment width. Length of segments: III

310–340, IV 340–310, V 370–380, VI 350–370, VII 310–330, VIII 310, IX 250, X 300. Segment X rather anodose, broad apically, with long setae not in whorls, with a few (4 or 5) antennal bristles on apex.

Thorax. Prothorax. Neck broad, equal to distance between compound eyes. Length 380. Dorsally: pronotum and pronotal sclerite absent. Post-tergites present, diagonal, each about 250 long. Laterally with a pair of distinct cervical sclerites, connecting with pleural ridges posteriorly.

Mesothorax. Dorsally: Prescutum transversely oval (length 240, width 150), scutum with an oval membranous area medially (length 210, width 130), lying behind prescutum. Scutellum triangular (length 160), scutoscuteellar sutures extending from the scutal membranous area postero-laterally to postalare; each exterior angle of scutellum with oval membranous areas. Prealare elongate; mesepisternite with a strong ridge on anterior margin.

Metathorax. metapostnotum Separated from scutellum by a large membrane. Details of other structures not visible as covered by wings dorsally, and a bubble ventrally. Only apex of postalare visible.

Wings. Fore wings large and well developed; 1310 long, 2770 wide (ratio of total body length to wing length 1 : 1.3 in holotype). Anterior membrane of wing above subcostal ridge sclerotized, surface of wing with characteristic monophlebid sculpture. Subcostal ridge reaching 2/3 along wing length. Cubital ridge shorter, ca. 3/4 of subcostal length, lying close to first light line. Both light lines present. First light line very long, reaching wing margin, bent; second light line shorter than cubital ridge. Point at which anterior light line reaches wing margin slightly indented. Alar lobe well developed. Hamulohalteres sclerotized, narrow, lanceolate (length 240, width 67), with 3 hamuli, each hooked.

Legs. Difficult to measure because of diagonal position of specimen, only lengths of fore legs measurable: coxae 210, trochanter + femur 620, tibia 610, tarsus (2-segmented) 320, claw 70. Morphology of legs very similar to those of *P. hoffeinatorum*; each coxa covered by many hair-like setae; each trochanter with several short and one long flagellate setae; femur with many setae, mostly short, but some along ventral and dorsal surfaces longer, up to 160, no bifurcated setae visible; tibia with numerous short bifurcated setae laterally and ventrally, longer flagellate setae present dorsally, with two tibial spurs, at distal apex of tibia. Tarsi 2-segmented, proximal segment very short and triangular; distal segment with a few bifurcated setae along ventral margin, and a few longer dorsal setae; tarsal digitules fine and setose. Claws straight and elongated, without denticle, with two fine digitules.

Abdomen. With a pair of caudal extensions present on segment VIII, each about 250 long, each with 3 very long, stout setae apically, and numerous shorter hair-like setae covering entire surface of each caudal extension. Details of remaining morphology not visible. Ventral surface hidden beneath a bubble; abdomen covered by wings dorsally.

TABLE 1. The list of fossil species of archaeococcoids recorded in Baltic amber.

Family Ortheziidae Amyot & Serville, 1843		
<i>Ochrycoris</i> Menge, 1856	<i>Ochrycoris electrina</i> Menge, 1843	female
<i>Arctorthezia</i> Cockerell, 1902	<i>Arctorthezia antiqua</i> Koteja & Žak-Ogaza, 1988	female
	<i>Arctorthezia baltica</i> Veá & Grimaldi, 2012	II instar larva
<i>Protorthezia</i> Koteja, 1987	<i>Protorthezia aurea</i> Koteja, 1987	male
<i>Palaeonewsteadia</i> Koteja, 1987	<i>Palaeonewsteadia huaniae</i> Koteja, 1987	male
<i>Newsteadia</i> Green, 1902	<i>Newsteadia succini</i> Koteja & Žak-Ogaza, 1988	female
Family Matsucoccidae Cockerell, 1927		
<i>Matsucoccus</i> Cockerell, 1909	<i>Matsucoccus pinnatus</i> (Germar & Berendt, 1856)	male, female, larva
	<i>Matsucoccus larssoni</i> Koteja, 1984	male, female
	<i>Matsucoccus electrinus</i> Koteja, 1984	male, female
	<i>Matsucoccus apterus</i> Koteja, 1984	male
Family Monophlebitidae Signoret, 1875		
<i>Monophlebus</i> Guérin-Méneville, 1827	<i>Monophlebus irregularis</i> Germar & Berendt, 1856	male
<i>Palaeophlebus</i> gen. n.	<i>Palaeophlebus hoffeinus</i> sp. n.	male
	<i>Palaeophlebus kotejus</i> sp. n.	male
Family Lithuanicoccidae Koteja, 2008		
<i>Lithuanicoccus</i> Koteja, 2008	<i>Lithuanicoccus damzeni</i> Koteja, 2008	male
	<i>Lithuanicoccus kosmowskiae</i> Koteja, 2008	male
Family Arnoldidae Koteja, 2008		
<i>Arnoldus</i> Koteja, 2008	<i>Arnoldus capitatus</i> Koteja, 2008	male
	<i>Arnoldus clavatus</i> Koteja, 2008	male
Family Kuwaniidae MacGillivray, 1921		
<i>Hoffeinsia</i> Koteja, 2008	<i>Hoffeinsia foldii</i> Koteja, 2008	I instar larva
Family Weitschatiidae Koteja, 2008		
<i>Weitschatus</i> Koteja, 2008	<i>Weitschatus stigmatus</i> Koteja, 2008	male
	<i>Weitschatus vysniauskasi</i> Koteja, 2008	male
Family Grohnidae Koteja, 2008		
<i>Grohnus</i> Koteja, 2008	<i>Grohnus eichmanni</i> Koteja, 2008	male
Family Serafinidae Koteja, 2008		
<i>Serafinus</i> Koteja, 2008	<i>Serafinus acutipterus</i> Koteja, 2008	male

Genital segment. Anus located between caudal extensions and surrounded by a sclerotized ring, observable only from ventral view. Penial sheath heavily sclerotized, 240 long, 80 wide, bilobed apically, extending beyond margins of abdominal segment VIII; aedeagus not clearly visible, but apparently with a bifid apex. Eversible endophallus not observed.

DISCUSSION

Based on the presence of caudal appendages and bifurcated setae on legs of the type species of *Palaeophlebus* we assign it to the family Monophlebitidae. According to the classification proposed by Morisson (1927, 1928), *Palaeophlebus* is very closely related to representatives of the tribe Monophlebini, based on the morphology of its antennae and abdomen. Antennal flagellomeres are irregularly nodose or irregularly trinodose with the setae not forming whorls as in *P. hoffeinorum* or just tend to cluster in three groups but definitely not forming distinct whorls of setae as in *P. kotejai*. Anodose structure of antennae with setae not forming whorls occurs in *Monophleboides gymnocarpi* (Hall, 1926) and *Monophlebidus indicus* Morrison, 1927 among Monophlebini. In *Labioproctus poleii* (Green, 1896) segments are irregularly trinodose and setae are not

arranged in distinct whorls. In Drosichini and Llaveiini segments of antennae are trinodose with three whorls of setae. In Monophlebulini and Iceryini antennal segments are binodose with two whorls of setae. Additionally, at the apex of the abdomen there is only one pair of caudal extensions, as in the Iceryini, but more than a single pair of these structures is characteristic of the Monophlebulini, Drosichini and Llaveiini. Penial sheath is very long, extending behind the middle margin of segment VIII (between caudal appendages), as in the Coelostomidiidae. Such an elongated, widened and bilobed at apex penial sheath is very distinctive in *Palaeophlebus*, but not found in extant males of Monophlebitidae.

In summary, the combination of the following morphological features: (i) irregular nodose or slightly trinodose structure of antennal segments with long setae not arranged in distinct whorls; (ii) first light line of wing long, reaching posterior wing margin, and with a short second light line; (iii) penial sheath elongated, strongly sclerotized and bilobed, extending beyond middle margin of abdominal segment VIII; and (iv) a single pair of medium-sized caudal appendages, that are not jointly found in recent genera, necessitates the creation of this new genus.

According to the online database of scale insects, ScaleNet (Ben-Dov et al., 2014), among the 240 species in 42 genera of the family Monophlebidae, the males of only 36 species have been described. The present study, therefore, increases the list of known monophlebid males and, also extends the list of archaeococcoids found in Baltic amber. Until now only 9 families with 22 species of archaeococcoids are described from Baltic amber, including 4 recent families – see Table 1 (Koteja, 1984, 1987a, b, 2008; Koteja & Żak-Ogaza, 1988a, b; Veá & Grimaldi, 2012).

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