The oldest jumping plant-louse (Hemiptera: Sternorrhyncha) with comments on the classification and nomenclature of the Palaeogene Psylloidea

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OUVRARD D., BURCKHARDT D. & GREENWALT D. 2013: The oldest jumping plant-louse (Hemiptera: Sternorrhyncha) with comments on the classification and nomenclature of the Palaeogene Psylloidea. In: KMENT P., MALENOVSKÝ I. & KOLIBÁČ J. (eds.): Studies in Hemiptera in honour of Pavel Lauterer and Jaroslav L. Stehlík. *Acta Musei Moraviae, Scientiae biologicae* (Brno) **98(2): 21–33**. – An Eocene compression fossil from the oil shales of the Kishenehn Formation in north-western Montana, USA, is described as *Eogyropsylla paveloctogenarius* sp.nov. It is the oldest known representative of the superfamily Psylloidea *sensu stricto* and the first Eocene (Lutetian, *ca.* 46 million year old) psyllid (Aphalaridae: Aphalarinae) from the New World. The world psyllid Paleogene fauna is reviewed, and the following nomenclatural acts and changes in the classification are proposed: *Carsidarina* Bekker-Migdisova, 1985 = *Palaeoaphalara* Klimaszewski, 1993 syn.nov.; *Proeurotica* Bekker-Migdisova, 1985 = *Plesioaphalara* Klimaszewski, 1993 syn.nov.; *Catopsylla* Scudder, 1890 = *Psyllites* Cockerell, 1915 syn.nov.; Paleopsylloidini Bekker-Migdisova, 1985 = Palaeoaphalarinae Klimaszewski, 1993 syn.nov.; *Parascenia* Klimaszewski, 1997 stat. rev., removed from synonymy with *Colposcenia* Enderlein, 1929; *Carsidarina* Bekker-Migdisova, 1985 transferred from the Carsidaridae to the Paleopsylloidini Bekker-Migdisova, 1985 (Aphalarinae); *Catopsylla* Scudder, 1890 transferred from the Psyllidae to the Paleopsylloidini.

Keywords. Aphalarinae, *Eogyropsylla*, jumping plant-lice, psyllids, fossil, biogeography, palaeontology, systematics, taxonomy, Holarctic Region, Kishenehn Formation

Introduction

Fossils provide a direct way of character polarisation when inferring phylogenies (OUVRARD *et al.* 2010). Fossils also document the diversification of morpho-anatomical structures through time, and help dating the age of lineages (HARBACH & GREENWALT 2012). A major problem with fossils is, however, that they are often incompletely preserved and that taxonomically important characters cannot be observed. This is also true in the jumping plant-lice or psyllids (Hemiptera: Sternorrhyncha: Psylloidea) where phylogenetically relevant characters are often difficult to observe (e.g., larval tarsal arolium) and homoplasy is important (e.g., presence/absence of a pterostigma in the forewing) (BURCKHARDT & QUEIROZ 2013).

Psyllids are small sap-sucking insects distributed worldwide. Most of the over 3850 described species (Li 2011) develop exclusively on dicotyledonous plants. Ouvrard *et al.* (2010) showed that Psylloidea *sensu stricto* are mainly characterised by the autapomorphic highly specialised metacoxa, with a striking development of its meron, on which the jumping muscles attach. The closest known lineages, without specialised coxa, forming the stem-group of extant Psylloidea are the extinct families Malmopsyllidae and Liadopsyllidae. The youngest known representative of Liadopsyllidae, *Liadopsylla hesperia* Ouvrard et Burckhardt, 2010, was described from the Upper Cretaceous (Turonian) and is *ca.* 90 million years (myr.) old.

After the extinction of the stem-group in the Late Cretaceous, the fossil record of Psylloidea *sensu lato* shows a gap of more than 46 myr. Fossil Psylloidea with modified coxae appear first in Baltic amber (Eocene). This gap covers almost exactly the time of the angiosperm radiation during the Upper Cretaceous and Paleocene. The simultaneous rarefaction in the psyllid fossil record, the explosion of flowering plant diversity and the appearance of modified morphological and biological traits in modern psyllids show how drastically the evolution and diversification of new plant families has influenced the evolution of Psylloidea. Together with the modification of the meral part of the metacoxa fused with the complex metathoracic furcae, the observed modified characters are the shortened rostrum, the robust femora, and the distally enlarged metatibiae bearing apical sclerotised spurs (Ouvrard *et al.* 2010).

The oldest described Psylloidea *sensu stricto* were found in Baltic amber dating from the Middle (44 myr.) to Upper Eocene (38 myr.) (Drohojowska & Szwedo 2011; Tables 1 and 2). These are the genera *Eogyropsylla* Klimaszewski, 1993, *Paleopsylloides* Bekker-Migdisova, 1985 and *Parascenia* Klimaszewski, 1997 (= *Colposcenia* Enderlein, 1929) which were assigned to the Paleopsylloidini (Aphalaridae: Aphalarinae) (Klimaszewski 2001), as well as *Protoscena* Klimaszewski, 1997, assigned to the Paurocephalinae (Rhinocolidae) by Klimaszewski (1997b). Klimaszewski (2001) defined the tribe Paleopsylloidini as follows: head lacking genal processes; vertex longer than half as wide; antenna 10-segmented, about as long as forewing width, with a subapical rhinarium on each of segments 4–9; clypeus subglobular; pronotum subrectangular; forewing with membranous pterostigma; hindwing with R+M; and male proctiger one-segmented with wing-like posterior processes. Considerably younger, from late Eocene or early Oligocene, are the genera *Carsidarina* Bekker-Migdisova, 1985, *Proeurotica* Bekker-Migdisova, 1985, *Lapidopsylla* Klimaszewski, 1993*, Plesioaphalara* Klimaszewski, 1993 and *Palaeoaphalara* Klimaszewski, 1993 which are all known from compression fossils from the Isle of Wight, UK. The first genus was referred to Carsidaridae (Bekker-Migdisova 1985), the last to the Palaeoaphalarinae (Aphalaridae), and the rest to the Paleopsylloidini (Klimaszewski 2001). The Palaeoaphalarinae were separated from Aphalarinae by the two-segmented male proctiger. The youngest Paleogene genera, at the Eocene/Oligocene border, are the three genera *Catopsylla* Scudder, 1890, *Necropsylla* Scudder, 1890 and *Psyllites* Cockerell,

1915 from Florissant, Colorado, USA, referred to the Psyllidae, Paleopsylloidini and Calophyidae, respectively (BEKKER-MIGDISOVA 1985, EVANOFF *et al*. 2001).

The Paleogene Psylloidea (Tables 1 and 2) have been referred to extinct genera of the extant families Aphalaridae, Calophyidae, Carsidaridae and Psyllidae (BEKKER-MIGDISOVA 1985, SHCHERBAKOV & POPOV 2002), unlike those from the Neogene which are morphologically close to or congeneric with extant genera (BURCKHARDT & OUVRARD 2012). In Dominican amber (Miocene) all extant families are represented except for Carsidaridae and Homotomidae (BURCKHARDT & OUVRARD 2012; D. Burckhardt, unpublished data).

Here we describe an Eocene compression fossil from the oil shales of Kishenehn Formation in north-western Montana, USA which we refer to *Eogyropsylla*. The attribution to a particular genus or even subfamily or family is difficult as many taxonomically relevant characters are missing and the systematics of Paleogene psyllids is in urgent need of revision. The new species is the oldest known representative of the superfamily Psylloidea *sensu stricto* and the first Eocene psyllid from the New World. In addition, known Paleogene taxa are discussed and their classification is reviewed.

Materials and methods

One female specimen was collected in 2012 at the Constenius Park site along the Middle Fork of the Flathead River under the auspices of United States Forest Service Permit HUN281. The specimen is deposited at the National Museum of Natural History in Washington, D.C. (USNM 553523).

The oil shale of the Middle Sequence of the Coal Creek Member of the Kishenehn Formation has been dated to 46.2 ± 0.4 million years old by 40Ar/39Ar analysis and 43.5 ± 4.9 million years old by fission-track analysis (CONSTENIUS 1996).

The age estimates are taken from the chronostratigraphic chart published by the International Commission on Stratigraphy in August 2012 (available at http://www.stratigraphy.org/).

The observation and photography were made after immersion of the specimen in 96% ethanol. Pictures were taken using a Canon EOS 50 D camera with a Macrolens MP-E 65 mm f/2.8 1–5X. Images were viewed with the software Canon EOS utility and stacked images were combined using the software Combine Z5.

The updated taxonomy together with literature and geological ages for fossils for all cited taxa can be found on the Psyl'list online database (OUVRARD 2013). Morphological terminology follows HOLLIS (2004).

Table 1. Paleogene Psylloidea according to the classifications of BEKKER-MIGDISOVA (1985) and KLIMASZEWSKI (1997b, 2001).

Family	Subfamily	Tribe	Genus species	Notes
Aphalaridae	Aphalarinae	Paleopsylloidini	*Eogyropsylla eocenica* Klimaszewski, 1993	Eocene, Baltic amber, Poland
			Eogyropsylla jantaria Klimaszewski, 1993	Eocene, Baltic amber, Poland
			Eogyropsylla magna Klimaszewski, 1997	Eocene, Baltic amber, Poland
			Eogyropsylla parva Klimaszewski, 1997	Eocene, Baltic amber, Poland
			Eogyropsylla sedzimiri Drohojowska, 2011	Eocene, Baltic amber, Poland
			Lapidopsylla memoranda Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
			Lapidopsylla thornessbaya Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
			Necropsylla rigida Scudder, 1890	Oligocene, Florissant, CO, USA
			Necropsylla rigidula Cockerell, 1911	Oligocene, Florissant, CO, USA
			Paleopsylloides oligocaenica (Enderlein, 1915) = *Strophingia oligocaenica*	Oligocene, Amber, Poland ("East Prussia")
			Parascenia weitschati Klimaszewski, 1997	Eocene, Baltic amber, Poland
			Plesioaphalara arcana Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
			Plesioaphalara inanima Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
			Plesioaphalara paulula Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
			Proeurotica exhumata (Cockerell, 1915) = *Psylla exhumata*	Eocene/Oligocene (Priabonian), Gurnet Bay, Isle of Wight, UK
		Palaeoaphalarinae	*Palaeoaphalara jarzembowskii* Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
			Palaeoaphalara media Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
			Palaeoaphalara ampla Klimaszewski, 1993	Eocene/Oligocene (Priabonian), Bembridge Marls, Isle of Wight, UK
	Aphalaroidinae	Aphalaroidini	*Camarotoscena? anglica* (Cockerell, 1915) = *Necropsylla anglica*	Oligocene, Gurnet Bay, Isle of Wight, UK
Carsidaridae	Calophyinae		*Psyllites crawfordi* Cockerell, 1915	Eocene/Oligocene, Florissant, CO, USA
	Carsidarinae	Carsidarini	*Carsidarina hooleyi* Cockerell, 1921	Oligocene, Gurnet Bay, Isle of Wight, UK
Psyllidae	Psyllinae		*Catopsylla prima* Scudder, 1890	Oligocene, Florissant, CO, USA
Rhinocolidae	Paurocephalinae		*Protoscena baltica* Klimaszewski, 1997	Eocene, Baltic amber, Kaliningrad, Russia

Taxonomy

Eogyropsylla paveloctogenarius sp.nov.   (Fig. 1)

Type locality. Park Middle Fork of the Flathead River 2 miles south of Stanton Creek, Montana, USA (W 113° 42.085′, N 48°23.517′).

Type material. Holotype: female, National Museum of Natural History in Washington, D. C. (USNM no. 553523).

Type stratum. Middle Eocene, Middle Sequence of the Coal Creek Member, Kishenehn Formation (Lutetian).

Description. A d u l t ,   f e m a l e . Body dark brown. Legs and forewing veins lighter brown. Thorax robust, strongly arched. Forewing ovoid, pterostigma absent, veins R and M+Cu subequal, vein R_1 long, almost perpendicular to vein Rs, cell cu_1 long and narrow. Abdomen large and hardly constricted at base. Metatibia relatively strong, barely expanding apically. Metabasitarsus enlarged. Apical tarsomere of hind leg bearing strong claws.

Head. In very bad condition, so that no constitutive part is visible with exception of the antennae and a portion of one eye. Nothing can be said about the shape of the genae nor the vertex. Antennae almost as long as forewing width, with two strongly enlarged basal articles. Segmentation of the flagellum not visible. Apical part slightly enlarged.

Thorax with sclerites visible from the side (laterally) caudally, but more from above frontally, because of a probable twisting of the anterior part of the body. Pronotum not visible. Mesopraescutum and mesoscutum large, subequal in length. Ventrally, part of the mesopleuron is visible, but strongly damaged. Second peritreme visible, as well as part of the pleural suture in mesothorax. Metathorax not visible, not distinguishable from the anterior segments of the abdomen.

Legs. Coxae not visible. Only apical portion of one hind leg visible. Tibia relatively long, more or less evenly thick throughout entire length, slightly thicker distally. Tarsus two-segmented, basal segment thick, expanded apically, distal segment ovoid, probably bearing two strong claws (one visible).

Forewing oblong-oval; 1.9 mm long, 0.9 mm wide. Only left forewing flat, as shown by the clearly visible and unfolded large anal cell (right wing probably slightly deformed

Table 2. Paleogene Psylloidea arranged according to geological epoch and stage.

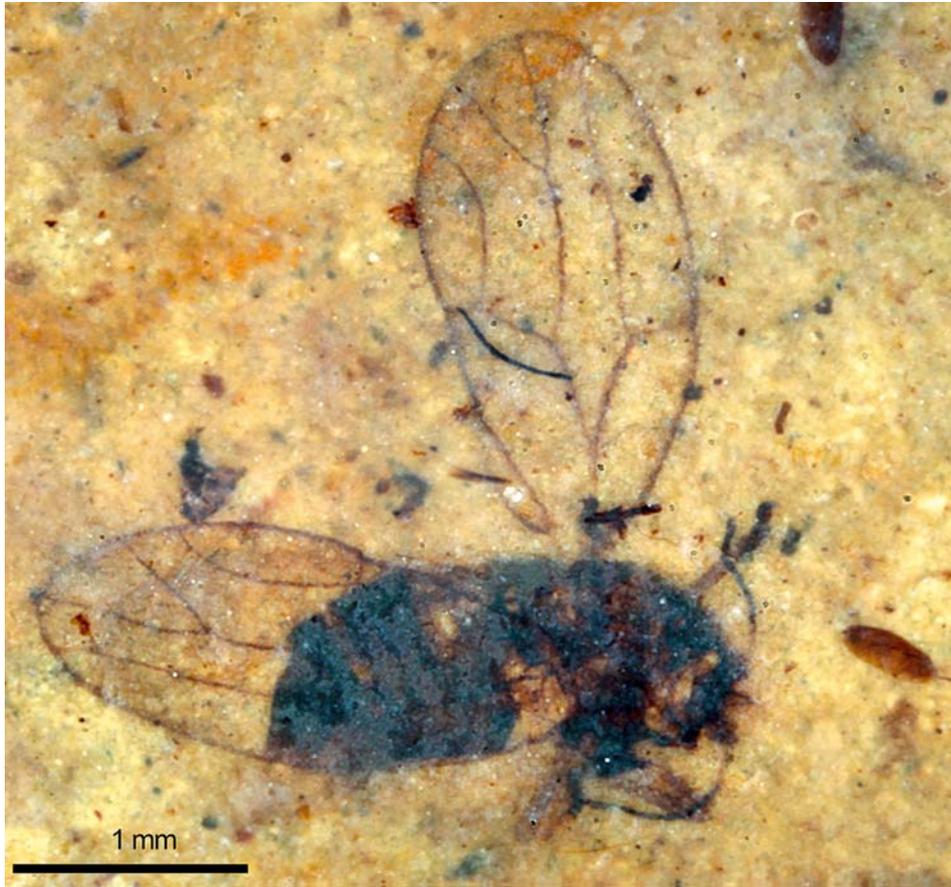| Geological epoch	Geological stage	Age (myr.)	Psyllid taxon
Eocene	Lutetian	47.8 - 41.3	*Eogyropsylla paveloctogenarius*
	Lutetian/Bartonian	47.8 - 38.0	*Eogyropsylla*
			Palaeopsylloides
			Parascenia
			Protoscena
	Priabonian/Rupelian	38.0 - 28.1	*Carsidarina*
			Lapidopsylla
			Proeurotica
Eocene/Oligocene	Priabonian/Rupelian	34.07	*Catopsylla*
			Necropsylla

Fig. 1. Female holotype of *Eogyropsylla paveloctogenarius* sp.nov. (USNM no. 553523).

during fossilization). Widest in apical third, without pterostigma nor visible thickening of vein C. Costal break present. Cell r_1 broad. Vein R_1 almost perpendicular to anterior wing edge, forming a right angle with vein Rs. Vein Rs sinuous and upturned at apex. Veins R and M+Cu subequal in length. Vein M hardly arched, vein M_{1+2} almost straight, in the prolongation of M, ending approximately at wing apex. Vein Cu 0.3 mm long. Cell cu_1 elongate, 2.45 times as long as high. Anal break present, adjacent to merging point of vein Cu_{1b} with posterior margin of the wing. A nodal line seems to be developed.

Hindwing not preserved.

Abdomen ovoid. Three large dark-brown distal tergites visible. Female terminalia cuneate. Proctiger 0.4 mm long, with straight dorsal margin. Anus 0.14 mm long.

M a l e . Unknown.

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Measurements. In μm. Total body length 1747, antenna length 630 (left) – 705 (right), forewing length 1906 (left) – 1942 (right), forewing width 936 (left) – 822 (right), vein R length 424, vein M+Cu length 406, vein M length 604, vein M_{1+2} length 486 (left) – 605 (right), vein M_{3+4} length 443 (left) – 441 (right), vein Cu length 294, cell Cu_1 length 617 (left) – 654 (right), cell Cu_1 height 252 (left) – 189 (right), abdomen length 1087, proctiger length 419, anus diameter 137.

Distribution. USA (Montana).

Etymology. Named in honour of our friend and colleague Dr. Pavel Lauterer on the occasion of his 80th birthday. Noun in apposition.

Differential diagnosis. *Eogyropsylla paveloctogenarius* sp.nov. is closest to *E. parva* Klimaszewski, 1997. The latter has a smaller body size with a longer cell m_1 and veins Rs and R_1 forming an acute angle in forewing, and with elongated female terminalia. The former differs from all other *Eogyropsylla* species in the absence of a pterostigma, the more rounded forewing shape, the elongated cell cu1 and the cuneate female terminalia.

Discussion

Compared to other insects, the fossil record of psyllids is scarce in general and completely lacking for the period from the late Upper Cretaceous (Coniacian) to the early Eocene (Ypresian). This paucity could be due to the minute body size of jumping plant-lice which can easily be overlooked during stone examinations but, more likely, it reflects a genuine rarity of psyllids during the Upper Cretaceous and the Palaeocene due to the profound changes in floras and climates bringing about the extinction of Liadopsyllidae and Malmopsyllidae followed by the development of a new group, the recent Psylloidea (KLIMASZEWSKI 1997a, 2001). The discovery of *Eogyropsylla paveloctogenarius* sp.nov. from Lutetian deposits is thus important, as it is the oldest representative of extant Psylloidea and it is the first New World psyllid known from the Eocene. Until now only two North American imprints of Aphalarinae were known from the Oligocene: *Necropsylla rigida* Scudder, 1890, and *Necropsylla rigidula* Cockerell, 1911, both from Florissant, Colorado, USA (the latter described from a very small forewing fragment). Two additional species from other families were described from the same stratum: *Psyllites crawfordi* Cockerell, 1915 (Calophyidae) and *Catopsylla prima* Scudder, 1890 (Psyllidae).

Eogyropsylla paveloctogenarius is placed in *Eogyropsylla* as it resembles the other species in the general body shape, the forewing venation and antennal length; other characters cannot be judged as they are not clearly visible. It differs from the remaining species in the lack of a pterostigma. Even though the presence or absence of a pterostigma is often stable within a genus, there are exceptions. In *Gyropsylla* (Aphalaridae, Aphalarinae) two species bear a membranous pterostigma, *G. cannela* (Crawford, 1925) and *G. ilicis* (Ashmead, 1881), and four lack one: *G. chiriquiensis* Brown et Hodkinson, 1988, *G. clypeata* Brown et Hodkinson, 1988, *G. longilabiata* (Li, 1991) and *G. speggazziniana* (Lizer, 1919). Within *Eogyropsylla*, *E. paveloctogenarius*

resembles most *E. parva* in the wing shape and dimensions. It differs from *E. parva* in the absence of a pterostigma and shorter female terminalia. KLIMASZEWSKI (1993) and DROHOJOWSKA (2011) recorded a well-developed pterostigma in *Eogyropsylla* species. The forewing of *E. parva* illustrated by KLIMASZEWSKI (1997a) lacks, however, a pterostigma but this is an error (holotype in Naturhistorisches Museum Basel, examined).

KLIMASZEWSKI (1993) placed *Eogyropsylla* in the extinct tribe Paleopsylloidini and suggested a close relationship to the extant genus *Gyropsylla* Brèthes, 1921. *Eogyropsylla* differs from *Paleopsylloides* in the forewing veins R and M+Cu which are of subequal length, rather than vein M+Cu distinctly longer that vein R. The latter state is relatively rare in psyllids and occurs for instance in many Spondyliaspidinae. Later, KLIMASZEWSKI (1997a) placed *Eogyropsylla* in the tribe Gyropsyllini. As stated by DROHOJOWSKA (2011), *Eogyropsylla* does, however, not share any derived character with *Gyropsylla*, and its phylogenetic relationship remains doubtful. Based on the presence of posterior processes on the male proctiger in *Paleopsylloides* and *Parascenia* their assignment to the subfamily Aphalarinae is well-supported. *Eogyropsylla*, only known from females and one last instar larva, resembles strongly the latter genus suggesting a close relationship. The monophyly of the tribe Paleopsylloidini is questionable as it is defined by likely symplesiomorphies and homoplasies (DROHOJOWSKA 2011). The tribe may be paraphyletic with respect to extant Aphalarinae whose internal phylogenetic relationships are also in need of revision (BURCKHARDT & OUVRARD 2012). DROHOJOWSKA (2011) suggested also that characters defining *Eogyropsylla* are symplesiomorphies, and *Parascenia* and *Paleopsylloides* are monotypic. The last differs from the first two genera in the wing venation but the first two are similar and may represent females and males of the same genus. KLIMASZEWSKI (1997a) stated that *Parascenia* is similar to *Colposcenia* in the enlarged lobes of the male proctiger, and BURCKHARDT & OUVRARD (2012) synonymised *Parascenia* with *Colposcenia*. Enlarged lobes occur also in other extant aphalarine genera such as *Caillardia*, and *Parascenia* differs from *Colposcenia* in the less inclined head which is angular rather that rounded anteriorly. More work is needed to confirm that *Eogyropsylla* and *Parascenia* are synonyms. We therefore suggest to reinstate the latter as *Parascenia* stat. rev. in the Paleopsylloidini. According to KLIMASZEWSKI (1997b) *Protoscena* lacks meracanthi. For this reason BURCKHARDT & OUVRARD (2012) assigned the genus to the Rhinocolinae (Aphalaridae).

The placement of the other Paleogene genera, known from impressions only, is difficult to judge as they consist often of single forewings. From the Isle of Wight, UK, compression fossils have been attributed to the genera *Carsidarina*, *Proeurotica*, *Lapidopsylla*, *Palaeoaphalara* and *Plesioaphalara*. *Carsidarina* and *Palaeoaphalara* share the short pterostigma, the short vein Cu_1 and the large cells m_1 and cu_1. We consider these characters as synapomorphies and suggest that the two are synonyms. The former was referred to the Carsidaridae (BEKKER-MIGDISOVA 1985) whose forewings differ considerably in the usually acute or subacute apex (except *Epicarsa*) (HOLLIS 1987) and the very small cell cu1. *Epicarsa* is characterised by Rs and M_{1+2} which are in broad contact. *Palaeoaphalara* was referred to the subfamily Palaeoaphalarinae (Aphalaridae)

on the basis of the two-segmented proctiger (KLIMASZEWSKI & POPOV 1993). Providing this observation is correct, it is probably a primitive character and unsuitable for phylogenetic reconstruction. The Palaeoaphalarinae was treated as *incertae sedis* by BURCKHARDT & OUVRARD (2012). It appears that Paleopsylloidini and Palaeoaphalarinae refer to the same group and we synonymise them and transfer *Carsidarina* to the Paleopsylloidini. Again there is a striking resemblance between the forewings of *Proeurotica* and *Plesioaphalara* in the small cell m_1 and very long cell cu_1, suggesting that they are congeneric. We propose here their synonymy. Among the youngest Paleogene genera *Catopsylla*, *Necropsylla* and *Psyllites* from Florissant, Colorado, USA, the first and last share an apically broadly rounded forewing with large m_1 and cu_1 cells indicating close relationship and synonymy of the two genera. They were attributed to the Psyllidae and Calophyidae, respectively, for neither of which is there any evidence. As the forewing characters resemble those of *Carsidarina* the taxon can be accommodated in the Paleopsylloidini.

Among Paleogene psyllids, *Eogyropsylla* and *Necropsylla* have several characters in common suggesting that they are more closely related to each other than either of them is to *Paleopsylloides*. Their type-species, viz. *E. eocenica* Klimaszewski, 1993 and *N. rigida*, share the following features: forewing oblong-oval, Rs long, cell r_1 very large, R and M+Cu of subequal length, M and M_{1+2} forming a relatively straight line, cell cu_1 elongate, and female terminalia cuneate. *Eogyropsylla* and *Necropsylla* differ from each other in the presence of a pterostigma in the former and a vein R_2 in the latter where the angle between R_1 and Rs is more acute. Unlike the Nearctic taxa, the Palaearctic *Eogyropsylla* species are all from Baltic amber (DROHOJOWSKA 2011) where much more morphological detail is visible than in compression fossils. There is also some doubt whether the pterostigma of *Eogyropsylla* and the presence of the vein R_2 in *Necropsylla* are in fact the same and just an artefact due to the differences in fossilisation (amber *versus* compression fossil). The assignment of *E. paveloctagenarius* to *Eogyropsylla* is supported by the similar age of these taxa, all from the Eocene. As reported by DROHOJOWSKA & SZWEDO (2011) the precise dating of Baltic amber is difficult and varies from Middle Eocene (ca. 44 myr. old) to Upper Eocene (ca. 38 myr. old). The Nearctic *Necropsylla* is considerably younger with an age difference of about 7 myr.

Regarding the biogeography, the newly described *Eogyropsylla* species extends considerably the distribution area of the genus, which was only known from the Old World until now. According to HODKINSON (1980), the development of a common fauna between Nearctic and the western Palaearctic, as pointed out also by KLIMASZEWSKI (1987), occurred until the final separation of the two regions, when the Atlantic corridor definitely closed in the Middle Eocene (ca. 40 myr. ago), which corresponds to the approximate age of our fossil and its congeneric species from Baltic amber. It means that the members of the genus in North America and the members in Europe had not been separated for a long time before their extinctions, which is corroborated by the fact that they do not show striking divergence in wing morphology, except for the absence of a pterostigma. Among the extant aphalarine genera, *Aphalara* Foerster, 1848 and *Craspedolepta* Enderlein, 1921, lack a pterostigma, and both have a Holarctic

distribution. Other Palaearctic genera containing species without a pterostigma are *Brachystetha* Loginova, 1964, *Crastina* Loginova, 1964, *Rhombaphalara* Loginova, 1964, and *Xenaphalara* Loginova, 1961. The following monotypic aphalarine genera restricted to the New World all have a pterostigma: *Limataphalara* Hodkinson, 1992; *Neaphalara* Brown et Hodkinson, 1988; *Hodkinsonia* Burckhardt, Espírito-Santo, Fernandes et Malenovský, 2004; and *Lanthanaphalara* Tuthill, 1959. The New World/Asian genus *Gyropsylla* which is associated with *Ilex* spp. (Aquifoliaceae) contains two described species with and four lacking a pterostigma. Being considered as an apomorphic state by KLIMASZEWSKI (2001), the lack of a pterostigma occurred probably several times independently all along the course of evolution of the Aphalarinae, and is hence of little phylogenetic significance.

According to HODKINSON (1980, 1992) the Neotropical aphalarine genera, apart from *Gyropsylla,* all monotypic, are relicts from a larger fauna, and the presence of *Gyropsylla* and *Limataphalara* in southern North America is due to more recent (less than 20 myr. old) northern migration from the Neotropics, together with other psyllid taxa. This biogeographic evidence is corroborated by the discovery of *E. paveloctogenarius* which does not share derived characters with *Gyropsylla*, contrary to the assumptions of KLIMASZEWSKI (1993, 2001) on which the name *Eogyropsylla* itself is based. This weakly supported relationship had already been impeded by the mention by KLIMASZEWSKI (1997b) of the affinity between *Gyropsylla* and *Protoscena baltica* (not a member of the Aphalarinae, but of the Rhinocolinae), which added confusion to the situation. As shown earlier, the lack of strong evidence for a close relationship between *Eogyropsylla* and *Gyropsylla* has already been mentioned by DROHOJOWSKA (2011).

Eogyropsylla is probably part of the stem-group which gave rise to the extant Aphalarinae genera. However, contrary to the Palaearctic, no diversification occurred in the Nearctic region, where the lineage of *E. paveloctogenarius* became extinct. In Eurasia, on the contrary, the diversification of the other members of the genus has gone on, and a centre of diversification occurred around Central Asia. Some of the genera reached North Africa in a South-Western expansion (e.g., *Caillardia* De Bergevin, 1931, *Colposcenia*, *Crastina*, *Rhodochlanis* Loginova, 1964), *Colposcenia* and *Crastina* even in the Afrotropical Region, while some others spread out on an Eastern track to the Far East (*Epheloscyta* Loginova, 1976) or were even able to cross the Beringia region at some point (*Aphalara* and *Craspedolepta*) as proposed by HODKINSON (1978, 1980).

The depositional environment of *E. paveloctogenarius* was both lacustrine and paludal; the exposures have an uncommonly large numbers of mosquito fossils (35 to date), two of which have recently been described (HARBACH & GREENWALT 2012). Other fauna described from the Formation include fishes, mollusks and vertebrates (CONSTENIUS *et al*. 1989, LI & WILSON 1994). The molluscan fauna of the Kishenehn Formation has been divided into four different successional groups, the first exemplified by *Gastrocopta miniscula* Pierce, 1992. *Gastrocopta pellucida* (Pfeiffer, 1840) selected as the extant analog of *G. miniscula*, currently lives in an environment characterized by a mean annual temperature of 25–27°C (PIERCE & CONSTENIUS 2001). The early arboreal primate *Tarkadectes montanensis* McKenna, 1990 originally described from the Coal Creek member (MCKENNA 1990), was recently assigned to the extinct family

Omomyidae (Nı *et al*. 2010). Most closely related to the Omomyidae are the insectivorous Tarsiidae, extant species of which are restricted to islands of Southeast Asia (Groves & Shekelle 2010). The temperatures of this period were significantly warmer than the present day and were likely wet subtropical in nature.

Although fossil leaves are moderately common in layers of siltstone and sandstone from the Kishenehn Formation, only very preliminary reports have been published (Ross 1959, Constenius *et al*. 1989). However, more detailed analyses of palynomorphs identified 27 different families of plants (Hopkins & Sweet 1976), but none of the common host-plant families for extant Aphalarinae (mainly Amaranthaceae, Asteraceae, Onagraceae, Polygonaceae and Tamaricaceae) has been reported from the site. The presence of fossil pollen from cattail (*Typha*) and waterfern (*Azolla*) support deposition in a paludal environment while the presence of abundant pollen of the family Pinaceae indicate the existence of a surrounding forested highland.

Nomenclatorial acts

Following new nomenclatorial acts are proposed here:

Carsidarina Bekker-Migdisova, 1985 = *Palaeoaphalara* Klimaszewski, 1993 **syn.nov.**

Proeurotica Bekker-Migdisova, 1985 = *Plesioaphalara* Klimaszewski, 1993 **syn.nov.**

Catopsylla Scudder, 1890 = *Psyllites* Cockerell, 1915 **syn.nov.**

Paleopsylloidini Bekker-Migdisova, 1985 = Palaeoaphalarinae Klimaszewski, 1993 **syn.nov.**

Parascenia Klimaszewski, 1997 **stat. rev.**, removed from synonymy with *Colposcenia* Enderlein, 1929

Carsidarina Bekker-Migdisova, 1985 transferred from the Carsidaridae to the Paleopsylloidini Bekker-Migdisova, 1985

Catopsylla Scudder, 1890 transferred from the Psyllidae to the Paleopsylloidini

Conclusion

The newly described fossil jumping plant-louse supports Grimaldi *et al*.'s (2002) observation that fossil insects from the Eocene belong almost exclusively to modern families, but not necessarily to modern genera. The exact relationships between the known Eocene fossils in Aphalarinae and the extant fauna are difficult to evaluate. The monophyly of Aphalarinae is reasonably well supported (Dobreanu & Manolache 1960, Burckhardt 1987) but not that of its five constituent tribes (Burckhardt & Ouvrard 2012, Burckhardt & Queiroz 2013). In addition there are no derived characters which would group the extinct members of the subfamily together with either the New World Aphalarinae or the Palaearctic ones. Furthermore, important diagnostic characters for defining aphalarine genera are not visible on rock imprints, like characters relating to the vertex, clypeus, hindlegs or the male terminalia. However, in extending the distribution of the genus to North America, the discovery of *E. paveloctogenarius* sp.nov., which is also the oldest member of the entire superfamily, allows specification of more detailed evolutionary scenarios for Aphalarinae that still have to be tested in a phylogenetic framework.

Acknowledgements

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