

# The fossil record of the planthopper family Achilidae, with particular reference to those in Baltic amber (Hemiptera: Fulgoromorpha)

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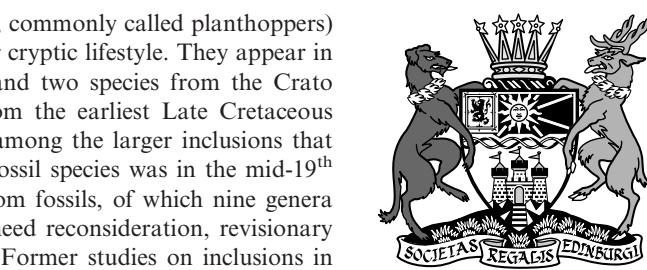
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**ABSTRACT:** The family Achilidae (Hemiptera, Fulgoromorpha, commonly called planthoppers) is one of the least known and least understood groups, due to their cryptic lifestyle. They appear in the fossil record in the Lower Cretaceous, with a single genus and two species from the Crato Formation of Brazil. The oldest amber inclusion is reported from the earliest Late Cretaceous amber of Burma. Surprisingly, Achilidae are relatively common among the larger inclusions that can be found in Eocene Baltic amber. The first description of a fossil species was in the mid-19<sup>th</sup> Century. Currently, there are 13 genera and 16 species known from fossils, of which nine genera and 11 species are from Baltic amber. However, many of them need reconsideration, revisionary studies and placement in the phylogenetic context of the family. Former studies on inclusions in this amber revealed several unique forms (extinct tribes Ptychoptilini and Waghildini), or taxa ascribable to the sparse Recent tribe Achilini. This paper provides an overview of the knowledge of fossil Achilidae, particularly those from Baltic amber. The Eocene appears to be the heyday of the family; however, this hypothesis should be tested with further detailed studies.

**KEY WORDS:** bugs, diversity, Eocene, taxa.

The Achilidae Stål, 1866 is one of the smaller families of planthoppers (Hemiptera: Fulgoromorpha), known from both extant and extinct taxa, and appeared in the fossil record in the Early Cretaceous. Due to their cryptic lifestyle and scarcity, it is one of the least known and least understood group of planthoppers. Currently, the family Achilidae comprises over 160 genera and about 550 species (Bourgois 2016), divided into three subfamilies (Achilixinae Muir, 1923a, Bebaiotinae Emeljanov, 1991 and Achilinae Stål, 1866), the latter with 11 Recent and two extinct tribes. Many of these tribes are poorly represented, often with just 1–2 specimens preserved in collections, often belonging to only one sex. There are still discussions on the classification and composition of the Achilidae (Emeljanov 1991, 1992; Urban & Cryan 2007; Bartlett *et al.* 2014).

The Achilidae are distributed worldwide, mainly in the tropical and subtropical zones (Metcalf 1948; Fennah 1950; O'Brien & M. R. Wilson 1985; O'Brien 2002); however, representatives of this family can range to high latitudes in the Northern Hemisphere, to the taiga zone, such as *Cixidia* (*Epiptera*) *lapponica* Zetterstedt, 1828, *C. (E.) slossonae* (Van Duzee, 1908) and *C. (E.) woodworthi* (Van Duzee, 1916) (Bartlett *et al.* 2014; Asche 2015). According to the biogeographical division of Holt *et al.* (2013), Achilixinae are known from the Oriental Region (the Philippines, Borneo, Celebes) and Bebaiotinae from the Panamanian Region (Ecuador, Guiana, Panama); whilst Achilinae are, in general, distributed worldwide, with a more limited distribution of particular tribes (e.g., Achilini in Africa, Australia and South America with a fossil record in Europe; Achillini from Africa with a fossil record in European deposits; Ilvini from Africa, Sevini from the Panamanian Region and Tropiphlepsini from Australia), with only Plectoderini widely dispersed from tropical to mild temperate zones of the world (Bourgois 2017).

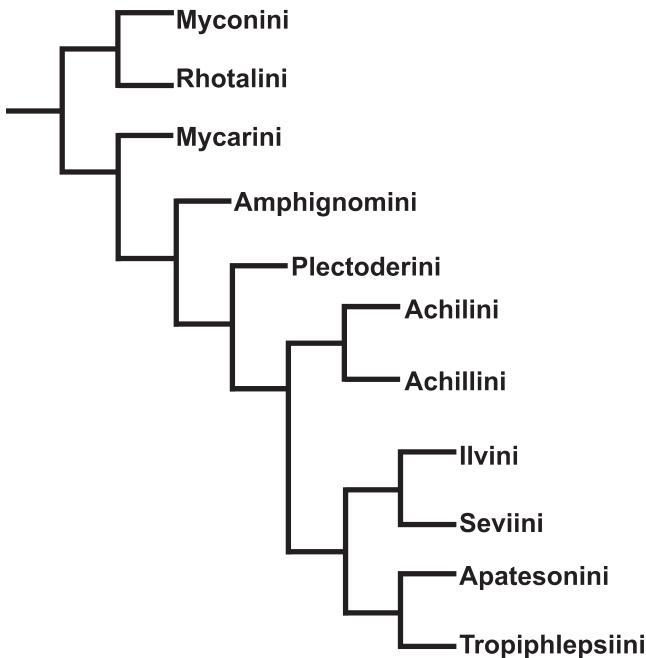


All Achilidae are phytophagous terrestrial insects. The biology of the group is insufficiently known; immatures are fungus feeders and are most easily found under the bark of dead logs (O'Brien 1971). Adults feed on woody plants, mostly they are reported as polyphagous (Wilson *et al.* 1994), but the degree of host specificity of adults is still not clear (O'Brien 1971; Asche 2015); they mainly feed on phloem of the host plants belonging to the gymnosperm families Pinaceae and Cupressaceae, and to the angiosperm orders Arecales, Asparagales, Asterales, Boraginales, Cuprales, Ericales, Fabales, Fagales, Hamamelidales, Lamiales, Laurales, Malpighiales, Malvales, Myrtales, Pinales, Poales, Rosales, Sapindales and Vitales (Wilson *et al.* 1994; Asche 2015; Bourgois 2017).

## 1. Fossil Achilidae

### 1.1. Family characters

Diagnostic features of Achilidae are: body usually dorsoventrally flattened, with tegmina held flat or tectiform, with their tips overlapped; clavus open, with claval veins  $P_{cu} + A_1$  running into CuP at the apex of clavus; head small, antennal pedicel globose; the second hind tarsomere with a row of spines (a feature shared with Cixiidae Spinola, 1839 and Kinnaridae Muir, 1925, which are the most similar families); in the male genitalia, the pygofer is flattened horizontally, often with median lobe, styles usually subquadrate, with aedeagal complex bilaterally symmetrical, consisting of periandrium surrounding an elongate paired rod-like penis, a connective is usually present between aedeagal base and the genital styles and inner walls of the pygofer; female genitalia modified to raking-kneading device enabling female to attach the eggs to particles of soil, decaying wood, or bark, with anterior connective lamina of gonapophyses



**Figure 1** Relationships of tribes in the subfamily Achilinae (after Emeljanov 1992 and Emeljanov & Fletcher 2004).

VIII bearing sturdy teeth, membranous endogonocoxal process and sclerotized endogonocoxal lobe; gonapophyses IX broadly fused basally, with distal tips pointed and gonoplacs with dorsal and ventral lobes, the latter bearing several sturdy bristles, exposed caudally.

The Achilidae is usually included amongst the group of Fulgoromorpha families referred to as ‘Cixiid-like’. Often, genera and species of Achilidae were mistaken for cixiid taxa. Though overlapping tegmina occurs in some representatives of other families (e.g., some Derbidae), it is generally a good way to recognise an achilid. The head capsule has vertex usually broader than long, with anterior margin more-or-less angulate or convex, and the disc slightly depressed, while the median carina is often obsolete or incomplete. The border between vertex and frons is sometimes callused. The frons, together with the postclypeus is, in most cases, elongate–ovate in outline, with lateral margins being carinate to foliate. Disc of frons is slightly convex to flattened, with median carina developed to various extent. The postclypeus is subtriangular, more-or-less flattened in profile, with the disk flattened or slightly convex. Median carina of postclypeus usually present, lateral margins carinate. However, many modifications and departures of this basic plan are observed. Antennae are typical for Fulgoromorpha, with enlarged, globular to suboval pedicel, with flattened star-shaped sensory plates, and thin flagellum. There are two ocelli located beneath the compound eyes, but achilids lack the third, median ocellus. Pronotum in general is little wider than head with compound eyes, short medially, usually with median disc, bounded laterally by carinae and with median carina. Lateral portions of pronotum variable, sloping down and anteriad of median disc. Mesonotum generally slightly broader than long in mid-line, more-or-less distinctly tricarinate. The tegulae are moderately large and bent through almost a right angle, sometimes carinate at line of flexure. Pro- and mesolegs bear no abnormal features in this family. Metatibiae usually bear lateral spine or spines and row of apical teeth; basimetatarsus is elongate, longer than middle one, middle metatarsus distinctly longer than broad, both with rows of apical teeth, sometimes with subapical setae; apical metatarsus with arolium well developed, a pair of wide dorsolateral sclerites and distinct tarsal claws. Tegmina usually

with membrane widened, overlapping at repose, membranous to slightly coriaceous. In the majority, the costal area not developed and pterostigma absent. Stem ScP + R + MP in most taxa leaving basal cell with a common stalk; stem ScP + R forked on corium; stem MP forked usually at level of nodal line, stem CuA forked on corium, basad of stem MP forking, branches CuA<sub>1</sub> and CuA<sub>2</sub> usually forked (at least one of them) subapically; long perpendicular to branch CuA<sub>2</sub> veinlet *icu* connecting CuA<sub>2</sub> and tornus (postclaval margin) present in majority of taxa. Clavus with apex obtuse and line of CuP prolonged as furrow on membrane. Hind wings usually wide, with venation developed variably, with basal cell present or absent, and variable venation of anal area (characters of taxonomic importance). Abdomen, in both males and females, is usually relatively short and depressed. Anal tube in most cases short and rounded (Fennah 1950; Anufriev & Emeljanov 1988; Asche 2015).

## 1.2. Taxonomic history and early fossil discoveries

The family Achilidae was erected by Stål in 1866 in his *Hemiptera Africana* under the name ‘Achilida’ (as a subfamily of the family ‘Fulgorida’), to include the 13 genera known at that time. The group was erected to the family level by Muir (1923b), although the spelling ‘Achilidae’ was first used by White (1879) as a subfamily of Fulgoridae. Muir (1923a) also established Achiliidae, as a separate family. The first subdivision of Achilidae into subfamilies (Apatesoninae and Achilinae) was proposed by Metcalf (1948), in his catalogue of the Hemiptera, with two and 76 genera included in the subfamilies respectively. The first author to attempt a full revision of this group was Fennah (1950), who divided the family into seven tribes: Rhotalini, Plectoderini, Myconini, Breddiniolini, Elidipterini, Achilini and Apatesonini. However, the current classification of Achilidae (Fig. 1) is mainly the result of major works by Emeljanov (1991, 1992), with subsequent updates (Emeljanov & Fletcher 2004), but these papers did not include fossils.

The first Achilidae fossils to be named were described by Germar & Berendt (1856); however, they were placed with other unrelated taxa in the family Cixiidae, all under the genus *Cixius* Latreille, 1807. It must be noted that these taxa (i.e., the genus *Cixius* and family Cixiidae), were a convenient ‘basket’ to place fossils without addressing classification or evolutionary issues, when they were described in the 19<sup>th</sup> and the beginning of the 20<sup>th</sup> centuries. Subsequent fossils (originally placed in the families Delphacidae and Derbidae) were described by Cockerell (1917, 1922). The first taxon to be placed in the family Achilidae was described from late Eocene deposits of Florissant (Scudder 1890) and the first extinct genus was described by Usinger (1939), from Baltic amber. Over the next 50 years, there were no descriptions of fossil achilids, nor any discussions or revisionary studies on them.

## 1.3. Renaissance of studies on Baltic amber and other fossils of Achilidae

Recent studies on fossil Achilidae commenced in 1990, when Emeljanov (1990) described a new genus and two species, representing a new extinct tribe of Achilidae from Baltic amber and Hamilton (1990) described a new extinct genus and two species from Lower Cretaceous deposits of the Crato Formation in Brazil. A few years later, Emeljanov (1994) transferred the genus *Hooleya* Cockerell, 1922 from the Derbidae to the Achilidae. Another fossil that was originally described by Cockerell (1917) from Burmese amber was transferred to the Achilidae as a new genus, *Niryasaburnia* Szwedo, 2004. The fossils of the family were critically reviewed, catalogued and

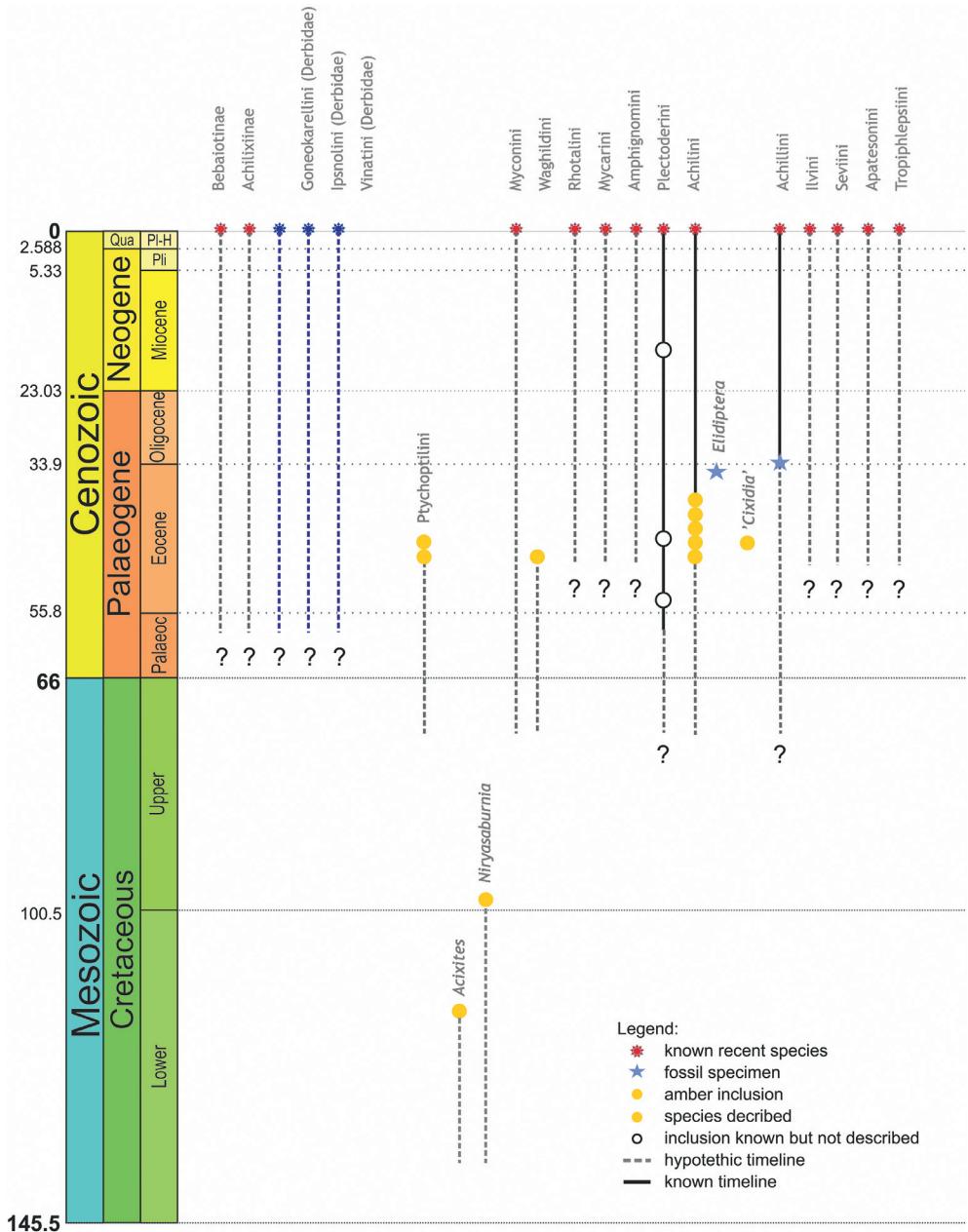


Figure 2 The fossil record of Achilidae subfamilies and tribes, and their presumed relatives.

discussed by Szwedo *et al.* (2004). A new fossil tribe from Baltic amber was described by Szwedo (2006) and several new genera and species from Baltic amber were described by Lefebvre *et al.* (2007) and Emeljanov & Shcherbakov (2009).

## 2. Fossil achilid genera and species

An annotated checklist (in alphabetical order) of the fossil Achilidae (Figs 2, 3), with some comments, is given below. This list complements Szwedo *et al.* (2004). The open nomenclature principles as proposed by Matthews (1973) and Bengtson (1988) are used.

Genus *Acixiites* Hamilton, 1990

\*1990 *Acixiites* Hamilton, p. 97.

.1992 *Acixiites* Hamilton; Hamilton, p. 429.

.2004 *Acixiites* Hamilton, 1990; Szwedo *et al.*, p. 41.

.2006 *Acixiites* Hamilton, 1990; Szwedo, p. 173.

.2007 *Acixiites* Hamilton, 1990; Szwedo, pp 298, 300.

**Type species.** *Acixiites immodesta* Hamilton, 1990, p. 97, by original designation.

**Remarks.** This genus belongs to subfamily Achilinae as tribe *incertae sedis*, as it cannot be placed in any of the currently recognized Achilinae tribes. With relatively simple venation, it is similar to some modern representatives of Plectoderini Fennah, 1950.

*Acixiites costalis* Hamilton, 1990

\*1990 *Acixiites costalis*: Hamilton, p. 97, Figs. 39, 42, 108, 109.

.2004 *Acixiites costalis* Hamilton, 1990; Szwedo *et al.*, p. 41.



**Figure 3** (A–C) Fossil Achilidae from Baltic amber: (A) *Angustachilus* sp., NHMUK In.18899, tribe Achilini; (B) *Ptychoptilum* sp., coll. Carsten Gröhn 5032, tribe Ptychoptilini; (C) *Waghilde baltica*, MNHN-LP-R AUF 061JS, tribe Waghildini. (D) Fossil Achilidae from Burmese amber: Achilinae, NIGPAS BA 04-16306, genus and tribe not yet identified.

- .2006 *Acixiites costalis* Hamilton, 1990; Szwedo, p. 167.
- .2007 *Acixiites costalis* Hamilton, 1990; Szwedo, p. 300, fig. 11.48.a.

**Occurrence.** Lower Cretaceous, late Aptian (*c.*114 Ma; Martill *et al.* 2007), Crato Formation, Ceará State, Brazil.

#### *Acixiites immodesa* Hamilton, 1990

- \*1990 *Acixiites immodesa* Hamilton, p. 97, figs 37, 38, 40, 41, 107.
- .2004 *Acixiites immodesa* Hamilton, 1990; Szwedo *et al.*, p. 41, fig. 3.
- .2006 *Acixiites immodesa* Hamilton, 1990; Szwedo, p. 167.
- .2007 *Acixiites immodesa* Hamilton, 1990; Szwedo, p. 300, fig. 11.48.c.

**Occurrence.** Lower Cretaceous, Aptian (*c.*114 Ma), Crato Formation, Ceará State, Brazil.

#### Genus *Angustachilus*

- \*2007 *Angustachilus* Lefebvre, Bourgoin & Nel, 2007, p. 41.
- .2009 *Angustachilus* Lefebvre, Bourgoin & Nel, 2007; Emeljanov & Shcherbakov, pp 1008, 1009.

**Type species.** *Angustachilus longirostris* Lefebvre, Bourgoin & Nel, 2007, p. 41, by original designation.

**Remark.** The genus is placed in subtribe Cixidiina Emeljanov, 1992 of the tribe Achilini Stål, 1866.

#### *Angustachilus longirostris* Lefebvre, Bourgoin & Nel, 2007

\*v2007 *Angustachilus longirostris* Lefebvre, Bourgoin & Nel, 2007, p. 42, figs 21–27.

2015 *Angustachilus longirostris* Lefebvre, Bourgoin & Nel, 2007; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (*c.*48–38 Ma), Baltic amber, Baltic coast, Poland.

**Remarks.** The age of Baltic amber is a subject of continuous debates (see Szwedo & Drohojowska 2016; Wolfe *et al.* 2016; Grimaldi & Ross 2017). The glauconites from ‘blue earth’ amberiferous Prussian Formation (the most productive mined horizon) were aged radiometrically by Ritzkowski (1997) as Lutetian. However, the reliability of this glauconite chronometer was argued by Clauer *et al.* (2005). Perkovsky *et al.* (2007) suggested a Bartonian/Priabonian age for the Prussian Formation, and this is also supported by the interpretations of Aleksandrova & Zaporozhets (2008) and Bogdasarov (2010). Grimaldi & Ross (2017), discussing the age of Baltic amber, concluded that the amber that comes from the ‘blue earth’

is most likely to be Priabonian in age. On the other hand, Ritzkowski (1999), Erichson & Weitschat (2008) and Matuszewska (2010) pointed out that Baltic amber is deposited in a marine environment, and that after the removal from the forest, the floating resin was transported south and redeposited together with fine-grained sands. Ritzkowski (1999) and Weitschat & Wicha (2010) mentioned that two additional amber-bearing horizons in the underlying beds of ‘blue earth’ indicate that amber had already been transported to secondary deposits about 50 million years ago. These statements for a Middle Eocene age of Baltic amber resin and its inclusions are supported by faunal links to the Middle Eocene Eckfeld Maar deposits of Germany (Wappler 2003; Wappler & Engel 2003); *Pleuarthropterus* (*Balticarthropterus*) Nagel, 1987 (Coleoptera: Carabidae: Paussinae) and the extinct bees (Hymenoptera: Apidae): *Protobombus* Cockerell, 1908 and *Electrapis* Cockerell, 1908 are taxa that have so far been found only in Baltic amber. Accordingly, we consider the age of fossils from the Baltic amber to be 48–38 Ma.

#### Genus *Elidiptera* Spinola, 1839

- 1966 *Elidiptera* Spinola, 1839; Metcalf & Wade, p. 100.
- 1992 *Elidiptera* Spinola, 1839; Carpenter, p. 238.
- 2004 *Elidiptera* Spinola, 1839; Szwedo *et al.*, p. 42.

**Type species.** *Elidiptera callosa* Spinola, 1839, p. 305, pl. 15, fig. 2; by monotypy.

**Remark.** The genus was placed in the tribe Achilini Stål, 1866, subtribe Elidipterina Fennah, 1950.

#### *Elidiptera regularis* Scudder, 1890

- \*1890 *Elidiptera regularis* Scudder, 1890, p. 297, l. XIX, fig. 13.
- .1906 *Elidiptera regularis* Scudder, 1890; Handlirsch 1906–08, p. 1068.
- .1939 *Elidiptera regularis* Scudder, 1890; Usinger, p. 65.
- .1966 *Elidiptera regularis* Scudder, 1890; Metcalf & Wade, p. 100.
- .1991 *Elidiptera regularis* Scudder, 1890; Lewis & Hikes, p. 220.
- .2003 *Elidiptera regularis* Scudder, 1890; Meyer, p. 207.
- .2004 *Elidiptera regularis* Scudder, 1890; Szwedo *et al.*, p. 42.
- .2006 *Elidiptera regularis* Scudder, 1890; Szwedo, p. 167.

**Occurrence.** Upper Eocene, Priabonian (c.34 Ma), Florissant, Teller County, Colorado, USA.

**Remark.** Only tentatively placed in this genus. The figure in Scudder (1890) is too unclear to resolve the placement.

#### Genus *Hooleya* Cockerell, 1922

- \*v1922 *Hooleya* Cockerell, 1922, p. 160.
- .1992 *Hooleya* Cockerell, 1922; Carpenter, p. 256.
- .1994 *Hooleya* Cockerell, 1922; Emeljanov, p. 76.
- .2004 *Hooleya* Cockerell, 1922; Szwedo *et al.*, p. 42.

**Type species.** *Hooleya indecisa* Cockerell, 1922, p. 160, by monotypy.

#### *Hooleya indecisa* Cockerell, 1922

- \*v1922 *Hooleya indecisa* Cockerell, 1922, p. 160, fig. 2.
- .1992 *Hooleya indecisa* Cockerell, 1922; Carpenter, p. 256
- .1994 *Hooleya indecisa* Cockerell, 1922; Emeljanov, p. 77, fig. 1a; pl. VII, figs. 1a, b.
- .2004 *Hooleya indecisa* Cockerell, 1922; Szwedo *et al.*, p. 42.
- .2004 *Hooleya indecisa* Cockerell, 1922; Szwedo, p. 105.
- .2006 *Hooleya indecisa* Cockerell, 1922; Szwedo, p. 167.

**Occurrence.** Upper Eocene, Priabonian (c.34 Ma), Insect Limestone, Solent Group, Isle of Wight, UK.

**Remark.** The genus and species were originally placed in family Derbyidae, but transferred to Achilidae, subfamily Achilinae and tribe Achillini Cockerell, 1922, by Emeljanov (1994). In the original description, the type locality is given as ‘Gurnet Bay’ (Cockerell 1922, p. 160). It is an old name for Gurnard Bay, but this was probably not where the specimen was found. The specimen probably came from Thorness Bay instead (Ross & Self 2014).

#### Genus *Niryasaburnia* Szwedo, 2004

- .1992 *Liburnia* Stål, 1866; Carpenter, p. 240.
- .2004 *Liburnia* Stål, 1866; Szwedo *et al.*, p. 94.

**Type species.** *Liburnia burmitina* Cockerell, 1917, p. 105, by original designation by Szwedo 2004, p. 105.

**Remark.** This genus belongs to the subfamily Achilinae as taxon *incertae sedis*, as it cannot be placed in any of the currently recognised Achilinae tribes.

#### *Niryasaburnia burmitina* (Cockerell, 1917)

- \*v1917 *Liburnia* (s. lat.) *burmitina* Cockerell, 1917, p. 329, figs 8, 9.
- .1920 *Liburnia burmitina* Cockerell, 1917; Fletcher, p. 988, pl. 166, figs 21, 22.
- .1966 *Liburnia burmitina* Cockerell, 1917; Metcalf & Wade, p. 113.
- .1982 *Liburnia* s. lat. *burmitina* Cockerell, 1917; Keilbach, p. 230.
- .1988 *Liburnia* s. lat. *burmitina* Cockerell, 1917; Spahr, pp 19, 48.
- .1990a *Liburnia burmitina* Cockerell, 1917; Lewis, p. 5.
- .1992 *Liburnia burmitina* Cockerell, 1917; Poinar, p. 125.
- .2000 ‘*Liburnia*’ *burmitina* Cockerell, 1917; Ross & York: 12, Fig. 7.
- .2000 ‘*Liburnia*’ *burmitina* Cockerell, 1917; Shcherbakov, p. 36.
- .2002 *Liburnia* (s. lat) *burmitinia* [sic] Cockerell, 1917; Szwedo, p. 52.
- .2004 *Liburnia burmitina* Cockerell, 1917; Szwedo *et al.*, p. 94.
- .2004 *Niryasaburnia burmitina* (Cockerell, 1917); Szwedo, p.106, fig. 1; pl. 1, fig. 4.
- .2006 *Niryasaburnia burmitina* (Cockerell, 1917); Szwedo, pp 167, 173.
- .2007 *Niryasaburnia burmitina* (Cockerell, 1917); Szwedo, p. 298.
- .2010 *Niryasaburnia burmitina* (Cockerell, 1917); Ross *et al.*, p. 232.

**Occurrence.** Upper Cretaceous, Cenomanian (*c.*99 Ma), Burmese amber, Hukawng Valley, Kachin State, Myanmar.

**Remarks.** The species was originally placed in the Recent Delphacidae genus *Liburnia* Stål, 1866. It was transferred to Achilidae by Shcherbakov (2000), but without a detailed redescription. The venation of this species is plesiomorphic and similar to that of Plectoderini Fennah, 1950 and Mycarini Emeljanov, 1991; however, the presence of platellae on the basi- and middle metatarsomeres excludes it from a close relationship with any representatives of these tribes. Double rows of subapical setae are to be found in Achilini Stål, 1866 and similar, platella-like structures are present in Tropiphlepsiini Emeljanov, 1991.

Genus *Paratesum* Emeljanov & Shcherbakov, 2009

**Type species.** *Paratesum rASNITSYNI* Emeljanov & Shcherbakov, 2009, p. 1009, by original designation.

**Remark.** The genus was placed in the tribe Achilini s.l., without subtribal assignation.

*Paratesum rASNITSYNI* Emeljanov & Shcherbakov, 2009

\*2009 *Paratesum rASNITSYNI* Emeljanov & Shcherbakov, 2009, p. 1011, l. 1, fig. 1, text-fig. 1a.

2015 *Paratesum rASNITSYNI* Emeljanov & Shcherbakov, 2009; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (*c.*48–38 Ma), Baltic amber, Gulf of Gdańsk deposit.

*Protepiptera* Usinger, 1939

\*1939 *Protepiptera* Usinger, 1939, p. 66.

.1950 *Protepiptera* Usinger, 1939; Neave, p. 223.

.1966 *Protepiptera* Usinger, 1939; Metcalf & Wade, p. 100.

1982 *Oliarius* [*sic*]; Keilbach, p. 230.

.1990b *Proteripiptera* [*sic*]; Lewis, p. 54.

1992 *Protepiptera* Usinger, 1939; Poinar, p. 124.

.1992 *Protepiptera* Usinger, 1939; Carpenter, p. 238.

.2004 *Protepiptera* Usinger, 1939; Szwedo *et al.*, p. 43.

2007 *Protepiptera* Usinger, 1939; Lefebvre, Bourgoin & Nel, pp 41, 43.

.2009 *Protepiptera* Usinger, 1939; Emeljanov & Shcherbakov, p. 1008.

.2009 *Protepiptera* Usinger, 1939; Emeljanov & Shcherbakov, pp 1008, 1009.

**Type species.** *Protepiptera kaweckii* Usinger, 1939, p. 66, by original designation.

**Comment.** The genus is placed in the tribe Achilini s.l., without subtribal assignation.

*Protepiptera kaweckii* Usinger, 1939

(?)\*1856 *Cixius longirostris* Germar & Berendt, p. 15, pl. I, fig. 22

(?)1891 *Cixius longirostris* Germar & Berendt, 1856; Buckton, p. 182, pl. G, fig. 22.

(?)1906 *Cixius longirostris* Germar & Berendt, 1856; Handlirsch, p. 1068.

(?)\*1910 *Oliarus oligocenus* Cockerell, 1910, p. 153.

(?)1938 *Oliarus oligocenus* Cockerell, 1910; Rodeck, p. 285.

\*1939 *Protepiptera kaweckii* Usinger, 1939, p. 66.

(?)1966 *Cixius longirostris* Germar & Berendt, 1856; Metcalf & Wade, p. 121.

(?)1966 *Oliarus oligocenus* Cockerell, 1910; Metcalf & Wade, p. 123.

(?)1982 *Cixius longirostris* Germar, 1856 [*sic*]; Keilbach, p. 230.

(?)1982 *Cixius longirostris* Germar & Berendt, 1856; Keilbach, p. 230.

(?)1982 *Oliarius oligocenicus* [*sic*] Cockerell, 1910; Keilbach, p. 230.

(?)1988 *Oliarus oligocenus* Cockerell, 1910; Spahr, p. 22.

.1990b *Protepiptera kaweckii* Usinger, 1939; Lewis, p. 54.

.1992 *Protepiptera kaweckii* Usinger, 1939; Carpenter, p. 238.

.2001 *Protepiptera kaweckii* Usinger, 1939; Szwedo & Stroiński, p. 95.

(?)2001 “*Cixius*” *longirostris* Germar & Berendt, 1856; Szwedo & Stroiński, p. 101.

2002 *Cixius longirostris* Germar & Berendt, 1856; Szwedo, p. 52.

2002 *Oliarus oligocenus* Cockerell, 1910; Szwedo, pp 45, 52.

.2002 *Protepiptera kaweckii* Usinger, 1939; Szwedo, p. 52.

?2004 *Cixius longirostris* Germar & Berendt, 1856; Szwedo *et al.*, p. 86.

\*v.2007 *Cixidia christinae* Lefebvre, Bourgoin & Nel, p. 39, figs. 10–20.

2007 *Protepiptera kaweckii* Usinger, 1939; Lefebvre, Bourgoin & Nel, p. 41.

.2009 *Protepiptera kaweckii* Usinger, 1939; Emeljanov & Shcherbakov, p. 1008.

2009 “*Cixius*” *longirostris* Germar & Berendt, 1856; Emeljanov & Shcherbakov, p. 1008.

2009 “*Oliarus*” *oligocenus* Cockerell, 1910; Emeljanov & Shcherbakov, p. 1008.

2009 *Cixidia christinae* Lefebvre, Bourgoin & Nel, 2007; Emeljanov & Shcherbakov, p. 1008.

2009? “*Cixius*” *longirostris* Germar & Berendt, 1856; Emeljanov & Shcherbakov, p. 1015.

2009? “*Oliarus*” *oligocenus* Cockerell, 1910; Emeljanov & Shcherbakov, p. 1015.

.2009 *Protepiptera kaweckii* Usinger, 1939; Emeljanov & Shcherbakov, pp 1015, 1016, pl. 2, figs. 1–3, text-fig. 2a–g.

2009 *Cixidia christinae* Lefebvre, Bourgoin & Nel, 2007; Emeljanov & Shcherbakov, p. 1015.

2015 *Protepiptera kaweckii* (Usinger, 1939) [*sic*]; Gröhn, p. 231.

2015 *Cixidia christinae* Lefebvre, Bourgoin & Nel, 2007; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (*c.*48–38 Ma), Baltic amber, ‘East Prussia’ [?], Sambia Peninsula: Kaliningrad Region, Russia; Gulf of Gdańsk, Poland.

*Protepiptera reticulata* (Germar & Berendt, 1856)

- \*p1856 *Pseudophana reticulata* Germar & Berendt, 1856, p. 16, pl. II, fig. 4 (pupa).
- p.1906 *Pseudophana reticulata* Germar & Berendt, 1856; Handlirsch 1906–08, p. 1070.
- p.1966 *Dictyophara reticulata* (Germar & Berendt, 1856); Metcalf & Wade, p. 126.
- p.1982 *Pseudophana reticulata* Germar, 1856; Keilbach, p. 229.
- p.1982 *Pseudophana reticulata* Germar in Berendt 1856; Keilbach, p. 229.
- p.1983 *Cixidia reticulata* (Germar & Berendt, 1856); Emeljanov, p. 79.
- p.1988 *Dictyophara (Pseudophana) reticulata* (Germar & Berendt, 1856); Spahr, p. 23
- p.2002 ‘*Pseudophana*’ *reticulata* Germar & Berendt, 1856; Szwedo, p. 48.
- p.2002 *Pseudophana reticulata* Germar & Berendt, 1856; Szwedo, p. 52.
- p.2004 ‘*Cixidia*’ *reticulata* (Germar & Berendt, 1856); Szwedo et al., pp 41–42.
- p.2009 “*Dictyophara* (= *Pseudophana*)” *reticulata* (Germar & Berendt, 1856; Emeljanov & Shcherbakov, p. 1008.
- 2011 *Protepiptera reticulata* (Germar & Berendt, 1856); Emeljanov & Shcherbakov, p. 177.
- 2015 *Protepiptera reticulata* (Germar & Berendt, 1856); Gröhn, p. 231.
- 2015 *Cixidia reticulata* (Germar & Berendt, 1856); Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c.48–38 Ma); Baltic amber, ‘East Prussia’ [?], Sambia Peninsula: Russia.

**Remarks.** On the basis of the original figures, Emeljanov (1983) argued that the “nymph” (Germar & Berendt 1856, pl. II, fig. 3) of *Pseudophana reticulata* Germar & Berendt, 1856 resembles nymphs of representatives of Tropiduchidae; whilst the “pupa” (Germar & Berendt 1856, pl. II, fig. 4) is similar to the nymphs of the genus *Cixidia* Fieber, 1866 species. The type material was probably lost during World War II, as it was sent to Königsberg in 1937. In the collection of Paläontologisches Institut Humboldt-Universität in Berlin, there is a single specimen labelled as ‘*Pseudophana reticulata*’, and its taxonomic status is under consideration. A lectotype for this species was designated by Emeljanov & Shcherbakov (2011, p. 177). These authors suggested that *Protepiptera reticulata* (Germar & Berendt, 1856) could possibly be a senior synonym of *P. kaweckii* Usinger, 1939.

Genus *Protomenocria* Emeljanov & Shcherbakov, 2009

**Type species.** *Protomenocria notata* Emeljanov & Shcherbakov, 2009, p. 1011; by original designation.

**Remarks.** The genus was originally placed in the tribe Achilini s.l., without subtribal assignment (Emeljanov & Shcherbakov 2009). Another species, originally described under the name *Cixius testudinarius* by Germar & Berendt (1856, p. 13, pl. I, fig. 19a, b), later moved to Achilidae by Usinger (1939), should probably be placed in this genus (Emeljanov & Shcherbakov 2009).

*Protomenocria notata* Emeljanov & Shcherbakov, 2009

\*2009 *Protomenocria notata* Emeljanov & Shcherbakov, 2009, p. 1014, pl. 2, fig. 4, text-fig. 1b–d.

- 2015 *Protomenocria notata* Emeljanov & Shcherbakov, 2009; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c.48–38 Ma), Baltic amber, Gulf of Gdańsk deposit.

**Remark.** Emeljanov & Shcherbakov (2009) noted that in analysed specimens, a variability in venation is observed, which could result in synonymisation of this species under ‘*Cixius*’ *testudinarius* Germar & Berendt, 1856.

Genus *Psycheona* Emeljanov & Shcherbakov, 2009

**Type species.** *Psycheona variegata* Emeljanov & Shcherbakov, 2009, p. 1016; by original designation.

**Remark.** The genus was originally placed in the tribe Achilini s.l., without subtribal assignation (Emeljanov & Shcherbakov 2009).

*Psycheona striata* Emeljanov & Shcherbakov, 2009

\*2009 *Psycheona striata* Emeljanov & Shcherbakov, 2009, p. 1018, pl. 1, fig. 4, text-fig. 3c.

2015 *Psycheona striata* Emeljanov & Shcherbakov, 2009; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c. 48–38 Ma); Baltic amber, Gulf of Gdańsk deposit.

*Psycheona variegata* Emeljanov & Shcherbakov, 2009

\*2009 *Psycheona variegata* Emeljanov & Shcherbakov, 2009, p. 1017; pl. 2, figs. 2–3; text-fig. 3a–b.

2015 *Psycheona variegata* Emeljanov & Shcherbakov, 2009; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c.48–38 Ma), Baltic amber, Gulf of Gdańsk deposit.

Genus *Ptychogroehnia* Szwedo & Stroiński, 2001

\*2001 *Ptychogroehnia* Szwedo & Stroiński, 2001, pp 95, 98.

.2004 *Ptychogroehnia* Szwedo & Stroiński, 2001; Szwedo et al., p. 43.

.2009 *Ptychogroehnia* Szwedo & Stroiński, 2001; Emeljanov & Shcherbakov, p. 1009.

**Type species.** *Ptychogroenia reducta* Szwedo & Stroiński, 2001, pp 95, 98; by original designation.

**Remark.** This genus is placed in the extinct tribe Ptychoptilini Emeljanov, 1990 (Szwedo & Stroiński 2001).

*Ptychogroehnia reducta* Szwedo & Stroiński, 2001

\*v2001 *Ptychogroehnia reducta* Szwedo & Stroiński, 2001, p. 98, figs. 5–10, 14–15.

.2002 *Ptychogroehnia reducta* Szwedo & Stroiński, 2001; Szwedo, p. 52.

.2004 *Ptychogroehnia reducta* Szwedo & Stroiński, 2001; Szwedo et al., p. 3, fig. 4.

.2015 *Ptychogroehnia reducta* Szwedo & Stroiński, 2001; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c. 48–38 Ma); Baltic amber, Gulf of Gdańsk deposit.

Genus *Ptychoptilum* Emeljanov, 1990

- \*1990 *Ptychoptilum* Emeljanov, 1990, p. 7.
- .2001 *Ptychoptilum* Emeljanov, 1990; Szwedo & Stroiński, p. 95.
- .2004 *Ptychoptilum* Emeljanov, 1990; Szwedo *et al.*, p. 43.
- .2009 *Ptychoptilum* Emeljanov, 1990; Emeljanov & Shcherbakov, pp 1008, 1009.

**Type species.** *Ptychoptilum major* Emeljanov 1990, p. 7; by original designation.

**Remark.** It is the type genus of the extinct tribe *Ptychoptilini* Emeljanov, 1990, so far known only from Eocene Baltic amber (Emeljanov 1990).

*Ptychoptilum major* Emeljanov, 1990

- \*1990 *Ptychoptilum major* Emeljanov, 1990, p. 10, fig. 1.
- .2001 *Ptychoptilum major* Emeljanov, 1990; Szwedo & Stroiński, p. 95, figs 1–3.
- .2002 *Ptychoptilum major* Emeljanov, 1990; Szwedo, p. 52.
- .2004 *Ptychoptilum major* Emeljanov, 1990; Szwedo *et al.*, p. 43.
- .2015 *Ptychoptilum major* Emeljanov, 1990; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c.48–38 Ma), Baltic amber, Gulf of Gdańsk deposit.

*Ptychoptilum minor* Emeljanov, 1990

- \*1990 *Ptychoptilum minor* Emeljanov, 1990, p. 9, fig. 2.
- .2001 *Ptychoptilum minor* Emeljanov, 1990; Szwedo & Stroiński, p. 95, fig. 4.
- .2002 *Ptychoptilum minor* Emeljanov, 1990; Szwedo, p. 52.
- .2004 *Ptychoptilum minor* Emeljanov, 1990; Szwedo *et al.*, p. 43.
- .2015 *Ptychoptilum minor* Emeljanov, 1990; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c.48–38 Ma), Baltic amber, Gulf of Gdańsk deposit.

Genus *Waghilde* Szwedo, 2006

- \*2006 *Waghilde* Szwedo, 2006, p. 168.
- .2009 *Waghilde* Szwedo, 2006; Emeljanov & Shcherbakov, p. 1009.

**Type species.** *Waghilde baltica* Szwedo, 2006, p. 168; by original designation.

**Remark.** It is the type genus for the extinct tribe *Waghildini* Szwedo, 2006, known exclusively, so far, from Eocene Baltic amber (Szwedo 2006).

*Waghilde baltica* Szwedo, 2006

- \*v2006 *Waghilde baltica*: Szwedo, 2006, p. 169, figs 1–13, 15–27.

- .2015 *Waghilde baltica* Szwedo, 2006; Gröhn, p. 231.

**Occurrence.** Eocene, Lutetian–Bartonian (c.48–38 Ma), Baltic amber, Gulf of Gdańsk deposit.

### 3. Summary – taxonomic issues and challenges

The investigation of Achilidae inclusions in Baltic amber has been going on for 160 years, but the group still is very challenging. There are several taxa already described which require revision; for example, some taxa described by Germar & Berendt (1856), placed formally in the genus ‘*Cixius*’ (Szwedo *et al.* 2004). The other challenge is the placement of the known fossil taxa into a phylogenetic context and classification scheme for the Achilidae. The question of the position and relationships of extinct tribes remains open. Despite new findings of fossils, analysis of relationships of the family and within the family, including fossil material, still awaits. Former studies on taxonomic diversity and morphological disparity of Baltic amber Achilidae revealed several unique forms, not present amongst Recent representatives of the family (such as the presence of the extinct tribes *Ptychoptilini* Emeljanov, 1990 and *Waghildini* Szwedo, 2006), or ascribable to taxa of low diversity. Surprisingly, most fossils from Baltic amber can be placed in the tribe *Achilini*. This tribe, in the Recent fauna, is represented by three subtribes (*Elidipterina* Fennah, 1950 (with 13 extant genera); *Achilina* Stål, 1866 (with four extant genera); and *Cixidiina* Emeljanov, 1992 (single extant genus, subdivided into two subgenera)) and nine extant genera unplaced to tribes (Asche 2015; Bourgoin 2017).

Precise biological data on Achilidae are scarce (O’Brien 1971; Bartlett *et al.* 2014; Wilson *et al.* 1994; Asche 2015; Bourgoin 2016), but it seems that at least some Recent species of the tribe *Achilini* have a close association with Fagaceae (*Quercus* spp., *Fagus* spp.) and Pinaceae (*Pinus* spp., *Abies* spp.) (Asche 2015), which could be an old association, possibly explaining their relative abundance amongst large Baltic amber inclusions. The trees of families and genera recognised as host plants of Achilidae were present in the Eocene amberiferous forests (Szwedo 2012). The Baltic amber forests were rich in decaying logs and twigs, creating suitable environments for the development of Achilidae nymphs. The trophic relationships of immatures, and partly of adults as sap-suckers, on the hyphae of fungi belonging to the Basidiomycota: Polyporales could be another reason for the incidence of these planthoppers in Baltic amber. These factors combined could result in a high taxonomic and morphological diversity of Achilidae, accounting for their frequent findings amongst large Baltic amber inclusions.

New efforts in collecting and studying specimens of Achilidae enclosed in Baltic amber are an essential prerequisite for any future analyses. The Achilidae seems to be a relic in the Recent fauna, and their taxonomic diversity is a result of a long evolutionary history. This hypothesis could be tested with detailed studies of the inclusions in Baltic amber and other Eocene deposits, the probable time of the Achilidae heyday. There are many unanswered questions on Recent Achilidae and many challenging issues regarding extinct Achilidae. This could be frustrating on the one hand, but on the other hand it makes studies on this group of insects very interesting.

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