



Spotted beauty—*Gedanochila museisucini* gen. et sp. nov.—a new Achilidae from Eocene Baltic amber (Hemiptera: Fulgoromorpha) and its relation to Achilini

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Abstract

Gedanochila museisucini gen. et sp. nov. is described, based on inclusions in the Eocene Baltic amber. A morphological phylogenetic analysis supports the placement of *Gedanochila* gen. nov. into the tribe Achilini. Definition, content and subdivisions of the tribe as well as position of extinct taxa placed within are briefly discussed.

Key words: *Gedanochila museisucini* gen. et sp. nov., Achilini, Eocene, inclusion, Baltic amber, planthopper

Introduction

Achilidae Stål, 1866 is one of the moderate-sized families of planthoppers, with 161 genera and 515 species respectively only counting for 6.5% and 3.7% of Fulgoromorpha diversity (Bourgoin 2022). The internal classification of the family is result of successive decisions, with first subdivision proposed by Metcalf (1938, 1948), followed by Fennah (1950), Emeljanov (1991, 1992) and Emeljanov & Fletcher (2004). However, the addition of two extinct tribes: Ptychoptilini Emeljanov, 1990 (Emeljanov 1990) and Waghildini Szwedo, 2006 (Szwedo 2006), and proposals to include Achilixiidae Muir, 1923 into Achilidae (Emeljanov 1991), to exclude them to Cixiidae (Liang 2001), or keeping them as a separate family (Urban & Cryan 2007), destabilized this classification. Currently, the classification of Achilidae includes 3 subfamilies and 11 recent and 2 extant tribes, while the placement of Ptychoptilini Emeljanov, 1990 remains unclear (Szwedo 2008; Brysz & Szwedo 2018, 2019; Emeljanov & Shcherbakov 2020; Bourgoin 2022).

Recent Achilidae are distributed worldwide, except for Arctic and Antarctic regions, reaching far north and south to earth's temperate zones, but with higher diversity in the northern subtropical and temperate zones (Bourgoin, 2022). Biology of species comprised in this family is very weakly known. Adults are supposed to suck phloem sap of trees and shrubs, and their nymphs, related to rotting wood, live under-bark; and presumably feed on fungal hyphae, possibly favouring Polyporales (O'Brien 1971, Asche 2015). In general, Achilidae seem more strongly associated with gymnosperms (Wilson *et al.* 1994) but they are also well linked with angiosperm Fagales and Ericales host plants (Bourgoin 2022), although adult plant associations remain unclear (Bartlett *et al.* 2018).

The fossil record of the family can be traced back to the Lower Cretaceous late Aptian deposits of Brazil (Hamilton 1990), making the family the second oldest planthopper extant taxon (ca. 115 Ma; Herrera-Flórez *et al.* 2020) in the Fulgoroidea (Szwedo *et al.* 2004, Brysz & Szwedo 2018, 2019; Szwedo 2018). The most common tribe represented among amber inclusions is Achilini (Lefebvre *et al.* 2007, Szwedo 2006, Emeljanov & Shcherbakov 2009; Brysz & Szwedo 2018, 2019), while several other fossil genera remain isolated in an *incertae sedis* position in the family classification (Bourgoin 2022). Because phylogenetically Achilidae is one of the basal families in Fulgoroidea (Bartlett *et al.* 2018; Brysz & Szwedo 2018, 2019), any new information allowing better documentation of the lineage and its evolution is of great importance for better understanding planthoppers evolution.

Within Achilinae, the tribe Achilini Stål, 1866 combines most of known fossil taxa. It is also the only tribe further divided into subtribes based on branching of anal veins in hind wings and presence of subapical setae on metatarsomeres (for key see Emeljanov 1992): Achilina Stål, 1866, Cixidiina Emeljanov, 1992 and Elidipterina Fennah, 1950 (Emeljanov 1992). Currently, subtribe Achilina has no fossil record and comprises only 4 known species, all placed in monospecific genera: *Achilus flammeus* Kirby, 1819, *Flatachilus diffinis* (Walker, 1858), *Olmiana argentina* Guglielmino, Bückle et Emeljanov, 2010 and *Ouwea doddi* Distant, 1907; subtribe Cixidiina comprises 1 recent genus: *Cixidia* Fieber, 1866 with a rather complex inner taxonomy, and 1 fossil *Angustachilus longirostris* Lefebvre, Bourgoïn & Nel, 2007; and the most numerous subtribe Elidipterina is composed of 12 genera, 7 of which are monospecific—*Metaphradmon* Fennah, 1950; *Paracatonidia* Long, Yang & Chen, 2015; *Paraphradmon* Fennah, 1950; *Parelidiptera* Fennah, 1950; *Phradmonicus* Emeljanov, 1991; *Prinoessa* Fennah, 1950 and *Uniptera* Ball, 1933, while the others comprises two (*Booneta* Distant, 1907 and *Messeis* Stål, 1862) or more species: *Elidiptera* Spinola, 1839—4; *Faventilla* Metcalf, 1948—5; *Catonidia* Uhler, 1896—10 (Bourgoïn 2022). Apart from these subtribes, the tribe Achilini comprises also 9 recent (among them 5 monospecific) and 4 fossil *incertae sedis* genera. The latter go as follows: *Protepiptera* Usinger, 1940 and *Psycheona* Emeljanov & Shcherbakov, 2009 with 2 species each, as well as monospecific *Protomenocria notata* Emeljanov & Shcherbakov, 2009 and *Paratesum rasnitsyni* Emeljanov & Shcherbakov, 2009.

Materials and methods

Material has been loaned from collection of Museum of Amber - Department of the Gdańsk Historical Museum, Gdańsk, Poland and from Centrum für Naturkunde (CeNak), Geologisch-Paläontologisches Institut, Hamburg Universität, Hamburg, Germany. No changes were made to the material without the approval of the collection's curator.

Observations and documentation were made using stereoscopic microscope Leica M205A. Photographs were taken using Leica DM6000 attached to Leica M205A microscope under control the LAS Montage multifocus and Helicon Focus 7.6.1 Pro software packages. Variable illumination was used to record as much information as possible (Savazzi 2011); additional anaglyph photographs were obtained with LAS Montage multifocus software. This kind of imaging allows to extract the maximum of information from an amber fossil (Haug J.T. *et al.* 2008, Haug C. *et al.* 2011, Hörnig *et al.* 2016). Observations and documentation were proceeded in the Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, University of Gdańsk. Photographs were readjusted using Adobe Photoshop Elements 6.0 and CorelPhoto-Paint X7 software packages. Drawings were made with camera lucida attached to Leica M2015A microscopes and readjusted with CorelDraw X7 package. To diminish distortions of image due to optical properties of amber and for more precise observations, specimens were placed under a thin layer of amber-friendly sugar solution and covered with a microscope slide.

Morphological terms used after proposals of Anufriev & Emeljanov (1988), Bartlett *et al.* (2014) and Asche (2015). Venation nomenclature based on Bourgoïn *et al.* (2015), with following abbreviations: Pc+CA, precosta + costa anterior; CP, costa posterior; ScP, subcosta posterior; R, radius; ScP+R(+MA), common portion of subcosta posterior, radius and media anterior; MA, media anterior is always fused with vein R (apomorphy of the Hemiptera), so we use here abbreviated notion ScP+R denoting this common stem (Bourgoïn *et al.* 2015); ScP+RA, common portion of subcostal posterior and radius anterior; RA, radius anterior; RP, radius posterior (with MA fused); MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; Pcu, postcubitus; and A₁, first anal vein. The naming and numbering of cells and areas of the tegmina is also based on Bourgoïn *et al.* (2015). The metatibiotarsal formula LT-(T)/Mt1/Mt2 provides the number of spines on the side of the metatibia (LT)—on the apex of metatibia, eventually in two groups of internal (Ti) and external (Te) spines separated with a diastemma (Ti-Te) / on the apex of first metatarsomere (Mt1) / on the apex of second metatarsomere (Mt2).

Modern world biogeographic divisions follow Holt *et al.* (2013). Palaeobiogeographic divisions for the Eocene based on Meyen (1987) and Akhmet'ev (2004), modified and updated with data and interpretations from Akhmet'ev & Zaporozhets (2014), Herold *et al.* (2014), de Bruyn *et al.* (2014) and Baatsen *et al.* (2020).

Both specimens come from the Eocene Baltic amber, from the area of Gulf of Gdańsk, most probably from the deposit in Sambian Peninsula, at Yantarnyi (Palmnicken). Baltic amber has been a subject of longstanding debates about its botanical origin, formation and age, about its accumulation and origin of its deposits. The biggest

concentration of amber in the deposit, in the Gulf of Gdańsk (Sambian Peninsula to Chłapowo), is definitively secondary one. For the discussion on age of the Baltic amber and its deposits see *e.g.*, Szwedo & Drohojowska (2016), Wolfe *et al.* (2016), Kosmowska-Ceranowicz (2017), Grimaldi & Ross (2017), Bukejs *et al.* (2019).

Phylogenetic analyses. Morphological data were compiled into Nexus files using Mesquite v. 3.61 build 927 (Maddison & Maddison 2019). The matrix was analysed using TNT v.1.5 (Goloboff *et al.* 2008, Goloboff & Catalano 2016), using Traditional Search option, with memory to store 99,999 trees, 10000 replications, with 100 trees to save per replication; utilizing tree-bisection-reconnection (TBR) algorithm and collapsing zero length branches, with *Aphypia* Melichar, 1908 (Plectoderini Fennah, 1950) designated as the outgroup. Equal weighting (EW) and implied weighting (IW) were used (Goloboff *et al.* 2008, Congreve & Lamsdell 2016), with concavity (k) values tested from 3 to 12 for IW analyses (Goloboff *et al.* 2018). The trees which maximize the concave function of homoplasy resolve character conflict in favour of the characters which have more homology (less homoplasy) and imply that the average weight for the characters is as high as possible. Though originally proposed with a severe weighting of k=3, more ‘gentle’ concavities (*e.g.*, k=12) seems to be suitable for morphological matrices comprising fossils (Goloboff *et al.* 2018). Branch support values were estimated using 10,000 bootstrap replicates. Obtained trees were viewed and had their features studied using WinClada 1.00.08 and ASADO 1.61 with Unambiguous Changes, Fast Optimization (ACCTRAN) and Slow Optimization (DELTRAN) options (Nixon 2002, 2004; Agnarsson & Miller 2008). Final tree files were adjusted using CorelDraw X7 package. Clades are named according to convention proposed by Amorim (1982).

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1946

Superfamily Fulgoroidea Latreille, 1807

Family Achilidae Stål, 1866

Subfamily Achilinae Stål, 1866

Tribe Achilini Stål, 1866

1866 Achilida: Stål, p. 130, 181 [*family*]

1904 Achilini: Swezey, p. 20 [*tribe*]

1950 Elidipterini: Fennah, p. 14, 22 [*tribe*]

1992 Alidipterini [sic!] Fennah, 1950: Yemel’yanov, p. 61 (Emeljanov 1992) [*tribe*]

***Gedanochila* Brysz et Szwedo, gen. nov.**

Type species. *Gedanochila museisucini* Brysz et Szwedo **sp. nov.**; by present designation and monotypy.

Etymology. Generic name is derived from Latin name of the city of Gdańsk ‘Gedanum’ and achilid planthopper generic name *Achila*. Gender: feminine.

Diagnosis. Vertex distinctly wider than long; separated by a transverse carina from frons, trigons absent; in lateral view the angle between vertex and frons blunt; loral suture oblique; labium short, reaching metacoxae. Pronotal disc elevated, arcuate, with lateral margins carinate; post-ocular carina absent. Metatibia with lateral spine at $\frac{2}{3}$ from base, with 10 apical teeth (some slightly shifted from base), basimetatarsomere longer than combined length of mid- and apical metatarsomeres, with subapical setae, midmetatarsomere with subapical setae. Stem ScP+R+MP leaving basal cell with a short common stalk. Stem MP forked at level of claval apex (stem MP forked apicad of claval apex in *Achilus* Kirby, 1818, *Olmiana* Guglielmino, Bückle et Emeljanov, 2010 and *Ouwea* Distant, 1907); stalk CuA₂ before fork on membrane short (in *Achilus* stalk CuA₂ long before fork on membrane), with two terminals (as in *Olmiana* and *Achilus*).

Age and occurrence. Lutetian, Eocene, Baltic amber, Gulf of Gdańsk area, secondary deposit.

Note. The new genus is placed in Achilini based on set of characters recognized by Emeljanov (1992): medium size, not enlarged or broadened head, prolonged frons with sides (sub)parallel, comparatively large pronotum, wider than head with compound eyes, disc of vertex carinate, tegmina slopingly tectate, with basal portion of costal margin arcuately convex, with enlarged costal cell, short common stem ScP+R+MP, stigmal area with crossveins, both branches of CuA forked on membrane, hind wing with RP branched, MP 3-branched, CuA 4-branched, metatibia with single lateral tooth in distal 1/3, basi- and midmetatarsomeres with subapical setae. See also discussion below.

***Gedanochila museisucini* sp. nov.**

(Figs 1–5)

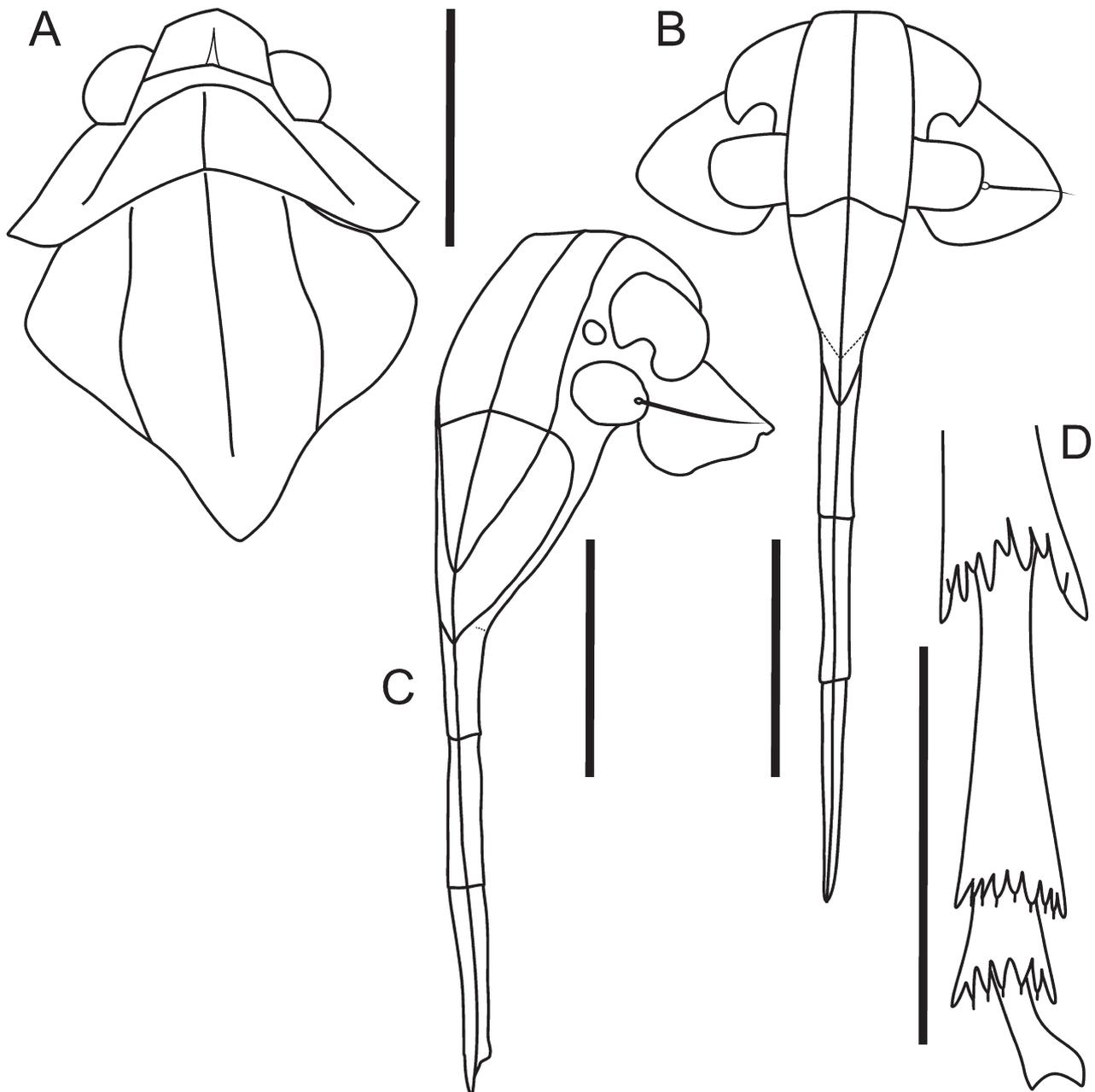


FIGURE 1. *Gedanochila museisucini* gen. et sp. nov. Holotype. A, Anterior portion of body in dorsal view; B, Head capsule in frontal view; C, Head capsule in frontolateral view; D, Tip of metatibia and metatarsus. Scale bar 1 mm.

Etymology. Specific epithet derived from Greek *museion*—museum, and Latin *sucinus*—amber, and refers to the Museum of Amber in Gdańsk.

Type material. Holotype. Specimen No. MHMB-827, deposited in Museum of Amber—Department of Museum of Gdańsk, Gdańsk, Poland. Piece of Baltic amber, with inclusion partly covered by milky veil and other impurities, which cover part of the head, most of the abdomen and parts of legs. **Paratype.** Specimen No. GPIH-SBS-0424, deposited in Centrum für Naturkunde (CeNak), Geologisch-Paläontologisches Institut der Hamburg Universität. Piece of amber, with inclusion partly covered with milky veil ventrally, right tegmen on layer with some mineral impurities (markasite?), one proleg detached; syninclusions: Microlepidoptera; isolated leg of Diptera (?).

Diagnosis. As for genus and in addition: pronotum $3.5\times$ as wide as long, tegmen with cell C5 slightly longer than cell C1; metatibio-tarsal formula LT2-10/Mt1-9(7)/Mt2-7(5); body dark, tegmina light, with regular colour pattern, with dark border at the tip and pterostigmal area, and two series of dots: three parallel to margin on costal cell, in the basal part of the wing and two on radial and median cells respectively, at basal $\frac{1}{3}$ of tegmen.

Description. Coloration. Body dark; tegmina light, with regular colour pattern (Figs. 3A, 4E-H, 5A), with dark border at the tip and pterostigmal area, and two series of dots: three parallel to margin on costal cell, in the basal part of the wing and two on radial and median cells respectively, at basal $\frac{1}{3}$ of tegmen.

Head. Head with compound eyes narrower than pronotum, about 0.6 as wide as pronotum. Vertex $2.5\times$ as wide as long in mid line. Anterior margin of vertex widely arcuately angulate, smoothly transiting to lateral margins, lateral margins diverging posteriad; posterior margin arcuately incised, reaching level of $\frac{1}{3}$ of compound eye length; all margins carinate; disc of vertex depressed, flat, with median carina widened at base, not reaching half of vertex length (Figs 1A, 3A, 4E-H, 4A, B). Frons in mid line $1.2\times$ as long as clypeus, $1.2\times$ as long as wide, subrectangular, with lateral margins slightly arcuate, slightly diverging ventrad; widest at level of antennal bases, laterally carinate; median carina distinct, reaching frontoclypeal suture. Frontoclypeal suture widely angulate. Postclypeus with distinct median carina, lateral carinae as prolongation of lateral margins of frons, converging ventrad, but not fused, anteclypeus about $2\times$ as long as wide at base (Figs. 1B, C, 4A, 5D). Rostrum reaching slightly behind base of metacoxae, apical segment longer than subapical one. Suture between gena and loral plate oblique. Compound eye with ventral incision, without subocular callosity. Lateral ocellus placed at level of lower margin of compound eye. Base of antenna below compound eye, scapus short, pedicel truncately subglobose, base of flagellum slightly inflated, flagellum about $4\times$ as long as pedicel (Figs. 1B, C, 2B, 3A, 5C, D).

Thorax. Pronotum $3.5\times$ as wide as long; disc in shape of depressed arch, elevated, not concave; lateral carinae not reaching posterior margin; posterior margin elevated, incised with an angle ~ 120 degrees. Mesonotum $1.2\times$ as wide as long, slightly humpy anteriorly, then sunken after half of its length, scutellum depressed; median carina not entering scutellum, lateral carinae full and straight (Fig. 1A, 3A, 4E-H, 5A, B)).

Metatibia with single lateral spine at $\frac{2}{3}$ of its length and with 10 apical teeth (6 in arcuate row and 4 based slightly above them). Basimetatarsomere with row of 9 apical teeth, basimetatarsomere distinctly (ca. $1.5\times$) longer than combined length of mid- and apical metatarsomeres; midmetatarsomere with row of 7 apical teeth; basi- and midmetatarsomeres bearing subapical setae, except lateral teeth. Metatibiotarsal formula LT2-10/Mt1-9(7)/Mt2-7(5) (Fig. 1D, 4B-D, 5E).

Tegmina and wings. Tegmina $3\times$ as long as wide; costal margin (fused veins Pc+CP+CA) curved at base than straight, strengthened at base, basal portion of Pc+CP carinate; anteroapical angle acutely rounded, posterior margin obliquely convex, posteroapical angle widely angulate, tornus merely convex; angle between A_2 and tornus ca. 160° . Basal cell narrow, about $4\times$ as long as wide, tapered apicad. Longitudinal veins elevated, stem ScP+R+MP leaving basal cell with a short common stalk, about $\frac{1}{2}$ length of basal cell, stem ScP+R forked at about $\frac{1}{3}$ of tegmen length, slightly basad to CuA fork, basad of claval veins junction; single prenodal branching (forked on left tegmen); branch ScP+RA with 5-6 terminals; branch RP with 3 terminals; branch MP with 7 terminals. Claval veins connecting at the level of ScP+R fork, slightly basad to CuA fork. Veinlet mp_4 -cua vein basad to rp - mp_1 , r one. Basal cell $4\times$ as long as wide; cell C1 more or less even in its width, curved; cell C5 lanceolate, with widened apical part. Cells C1/C3 length ratio 1.58; cells C1/C5 length ratio 0.98; apical line parallel to wing margin in apical part, then convex; apical cells narrow. Membrane covering about 40% of tegmen's length (Fig. 2A, B; 3A, B, 4E-H, 5A, C).

Venation differs in both tegmina—left tegmen: branch RA with 7 terminals (6 terminals on right tegmen); RP with 4 terminals (3 terminals on right tegmen), branch MP_{1+2} forked slightly apicad of branch MP_{3+4} forking (branch MP_{1+2} forked much more basad of branch MP_{3+4} forking on right tegmen); branch MP_4 forked twice, resulting in 8 terminals of MP, with branching MP_{4b} intercepted by terminal CuA_1 in apical section (7 terminals of MP on right

tegmen); cell C3 closed with double crossvein near its base, at level of nodal line, cell C3a with crossvein in the middle, cell C4' tapering and divided by a crossvein in apical part, cell C5 with one complete crossvein on the narrowing and one incomplete in basal part; right tegmen: RA with 5 terminals, additional recurrent vein between MP and CuA stems in cell C4, cell C1 with oblique additional veinlet before half of its length (Fig. 2A, B; 3A).

Hind wing. Anteroapical angle widely angulate. ScP+RA single reaching margin distinctly basad of apex, branch RP vein with 2 terminals (3 terminals on the left hindwing), reaching margin basad of apex; stem MP with 3 terminals (MP₃₊₄ not branched), terminal MP₂ forked before margin on left hindwing; branch CuA with 4 terminals, CuA₁ forked, CuA₂ single, CuP not branched. Veinlet *rp-mp* long, reaching stem MP slightly basad of MP forking, veinlet *mp-cua*₁ merely basad of *rp-mp* veinlet, in line with stalk of CuA_{1b}. Anal region not visible (Fig. 2C, D; 3A, B. 5A, C).

Age and occurrence. Lutetian, Eocene, Baltic amber, Gulf of Gdańsk area, secondary deposit. For the discussions on age of the Baltic amber and its deposits see *e.g.*, Szwedo & Drohojowska (2016), Wolfe *et al.* (2016), Grimaldi and Ross (2017), Bukejs *et al.* (2019), Sadowski *et al.* (2017, 2020).

Phylogenetic analysis

Characters list

Head

1. Rostrum: 0—reaching to end of metacoxae; 1—reaching to base of metacoxae or shorter; 2—exceeding metacoxae
2. Vertex length/width ratio: 0—less than 2×; 1—equal or more than 2×
3. Shape of vertex: 0—trapezoid; 1—semicircular; 2—narrowly band-like
4. Lateral margins of frons in dorsal view: 0—strongly exceeding anterior margin of frons/vertex; 1—not exceeding anterior margin of frons/vertex
5. Posterior margin of vertex in lateral view: 0—elevated; 1—not elevated
6. Disc of vertex 0—not concave; 1—concave
7. Lateral margins of frons: 0—margins not distinctly elevated; 1—margins elevated, foliate
8. Frons shape: 0—subquadrate; 1—subhexagonal
9. Frons length/width ratio: 0—up to 1.5; 1—over 1.6
10. Disc of frons: 0—flat; 1—concave
11. Clypeal suture: 0—straight; 1—arcuate; 2—arcuate, outstretched upwards
12. Disc of clypeus: 0—convex; 1—flat; 2—concave
13. Lorai plates in frontal view: 0—not visible; 1—visible
14. Compound eye: 0—without antennal indentation; 1—with antennal indentation
15. Pedicel: 0—subglobose; 1—elongated, twice as long as wide

Pronotum

16. Pronotum: 0—normal sized, fully visible; 1—reduced in length, partially covered by vertex
17. Disc of pronotum in caudal view: 0—flat; 1—roof-like, medially elevated
18. Lateral carinae of pronotal disc: 0—straight; 1—curved
19. Pronotal median carina: 0—not elevated; 1—elevated, crest-like
20. Pronotal posterior margin in lateral view: 0—elevated; 1—not elevated

Mesonotum

21. Mesonotal lateral carinae: 0—straight; 1—curved; 2—S-like

Tegmen

22. Tegmen total length/width at claval apex: 0—up to 3×; 1—more than 3.1×
23. Pterostigmal crossveins: 0—all anterodistal; 1—not
24. RA terminals: 0—up to 4; 1—5; 2—more than 5
25. RP vein terminals: 0—1; 1—2; 2—3 or more

26. MP vein terminals: 0—4-5; 1—3; 2—6 or more
27. Basal cell ratio: 0—less than 4×times as long as wide; 1—more than 4× as long as wide
28. Cell C1 in apical portion with borders: 0—converging apicad; 1—subparallel apicad
29. Cell C5 shape: 0—with margins subparallel; 1—lanceolate, with margins sigmoid
30. Membrane length: 0—more than 50% of forewing length; 1—less than 50%

Hind wing

31. Anastomosis of anal veins: 0—absent; 1—present
32. Blind branches in anal veins anastomosis: 0—absent; 1—present
33. Median fold in hindwings: 0—present; 1—absent

Metalegs

34. Subapical setae present on metatarsomeres: 0—present; 1—absent
35. Subapical setae: 0—on both tarsomeres; 1—on mid-metatarsomere

Our first analysis was based only on taxa ascribed to the subtribe Achilina Stål, 1866 (*i.e.*, genera *Achilus* Kirby, 1818, *Flatachilus* (Walker, 1858), *Gedanochila* **gen. nov.**, *Olmiana* Guglielmino, Bückle et Emeljanov, 2010 and *Ouwea* Distant, 1907) with 2 genera used as outgroups: *Aphypia* Melichar, 1908 as a representative of tribe Plectoderini (subfamily Myconinae), and *Cixidia* Fieber, 1866 as representative of presumed sister subtribe—Cixidiina Emeljanov, 1992 (Achilini Stål, 1866).

Due to unresolved basal polytomy, the matrix was expanded with one more outgroup, the genus *Apateson* Fowler, 1900 from different subfamily (Apatesoninae), together with other representatives of Achilinae subfamily: 2 representatives of other Achilini subtribes—extinct *Angustachilus* Lefebvre, Bourgoïn et Nel, 2007 of subtribe Cixidiina, and extant genera *Faventilla* Metcalf, 1948 and *Parelidiptera* Fennah, 1950 of subtribe Elidipterina; as well as other extinct genera from the Eocene Baltic amber placed as Achilini *incertae sedis*—*Paratesum* Emeljanov et Shcherbakov, 2009, *Protepiptera* Usinger, 1940, *Protomenocria* Emeljanov et Shcherbakov, 2009 and *Psycheona* Emeljanov et Shcherbakov, 2009. Full matrix is presented in Table 1.

New Technology Search with equal weighting resulted in 4 trees, 131 steps long, consistency index $Ci = 32$, retention index $Ri = 40$. Resulting strict consensus tree is poorly resolved, 167 steps long, $Ci = 25$, $Ri = 16$, with topology [*Apateson* + [*Flatachilus* + [*Protomenocria* + [[*Protepiptera*, *Achilus*, *Olmiana*, *Ouwea*, *Gedanochila*, *Faventilla*, *Parelidiptera*, *Cixidia*, *Angustachilus*, *Psycheona* + [*Aphypia* + *Paratesum*]]]]]. Resulting majority rule tree is also poorly resolved, 153 steps long, $Ci = 27$, $Ri = 25$, with topology [*Apateson* + [*Flatachilus* + [*Protomenocria* + [[*Aphypia* + *Paratesum*] + [[*Achilus*, *Olmiana*, *Ouwea*, *Faventilla*, *Parelidiptera*, *Cixidia*, *Angustachilus*, *Psycheona* + [*Protepiptera* *Gedanochila*, *Angustachilus*]]]]]]].

New Technology Search with implied weighting and various values of parameter k (concavity), between 3 and 12, these analyses resulted in single trees. The most parsimonious tree received, with k parameter 12 is presented in Fig. 6A. It is 131 steps long, consistency index 32, retention index 40, and high number of characters revealed as homoplastic. The extinct genus *Paratesum*, placed originally in Achilini, appeared as sister to genus *Aphypia* (Plectoderini)—*Aphypia*+ clade, supported only by homoplastic characters. The clade uniting other extinct genera (except *Protomenocria*) and representatives of Recent Achilini (*Angustachilus*+) is supported by synapomorphies 9(0), 12(1) and 20(1). Two clades are present, first supported only by homoplastic characters with [*Angustachilus* + [*Protepiptera* + *Gedanochila*]]—extinct genera and second clade *Ouwea*+, supported by single synapomorphy 13(1). This clade contains [*Ouwea* + [*Faventilla* + *Parelidiptera*]] supported by single synapomorphy 34(1) [*Cixidia* + [*Olmiana* + [*Achilus* + *Psycheona*]]], supported by homoplastic characters. For all nodes bootstrap values are low.

If our analysis supports Achilini monophyly, the subtribal divisions proposed by Emeljanov is not recovered. This could be explained by high load of homoplastic characters. Diagnostic features proposed for the subtribes by Emeljanov (1992) seems to be useful for recognition of taxa, but not for phylogenetic reconstructions. Perhaps, a larger analysis including all genera might also result with another topology, however many genera placed in Achilini, especially in Elidipterina, remain very weakly known in terms of their characters, often also from singletons only in the collections.

Table 1. Matrix of characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
<i>Apateson</i>	1	0	2	0	1	0	1	1	1	1	1	2	0	0	0	1	-	0	1	1	1	0	1	2	1	0	0	1	0	1	0	-	1	0	1	
<i>Aphygia</i>	0	1	0	1	1	0	0	1	0	1	1	0	0	1	0	1	1	1	0	1	0	1	1	0	1	1	1	0	1	0	-	1	0	0	0	
<i>Proteptera</i>	2	0	1	1	1	1	0	1	1	0	1	1	0	0	0	0	1	0	1	1	2	1	1	0	2	2	1	0	1	1	1	1	1	1	0	0
<i>Achilus</i>	1	0	0	1	1	1	0	1	1	1	2	2	0	0	1	0	0	1	1	0	0	0	0	1	2	0	0	0	1	0	1	1	1	0	1	
<i>Flatachilus</i>	?	0	0	0	1	1	0	1	1	1	2	0	0	0	1	0	1	1	-	1	-	0	1	2	1	2	0	1	0	0	1	0	1	0	1	
<i>Olmiana</i>	0	1	0	1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	0	0	2	1	0	2	1	1	1	0	1	1	1	1	1	0	1	
<i>Ouwea</i>	1	1	2	1	0	1	0	1	0	0	2	1	1	0	1	0	0	1	0	0	0	1	1	2	2	2	0	0	1	1	0	0	1	1	-	
<i>Gedanochila</i>	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	2	0	1	1	2	2	0	1	0	1	?	?	1	0	0	
<i>Faventilla</i>	0	0	0	1	0	1	0	1	1	0	1	2	1	0	0	0	0	0	1	0	0	0	1	2	1	0	0	1	1	1	?	?	0	1	-	
<i>Parelioptera</i>	0	1	0	0	1	1	0	1	0	1	2	1	1	1	0	0	1	1	1	0	2	0	1	1	2	2	1	0	1	1	1	1	0	1	-	
<i>Cixidia</i>	1	0	0	1	1	1	0	1	0	0	1	0	1	0	1	0	1	1	1	0	1	1	0	0	2	2	0	1	1	1	1	1	0	0	0	
<i>Angustachilus</i>	2	1	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	0	1	0	1	1	1	1	2	0	0	0	1	1	1	1	1	0	0	
<i>Paratesum</i>	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	1	2	0	0	0	1	0	?	?	?	0	1	
<i>Psycheona</i>	2	0	0	1	0	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	1	1	0	0	2	2	1	0	0	1	?	?	?	0	1	
<i>Protomenocria</i>	0	0	0	0	0	1	1	0	1	1	1	0	0	0	1	0	1	1	0	1	1	1	0	0	2	0	0	0	1	1	?	?	1	0	0	

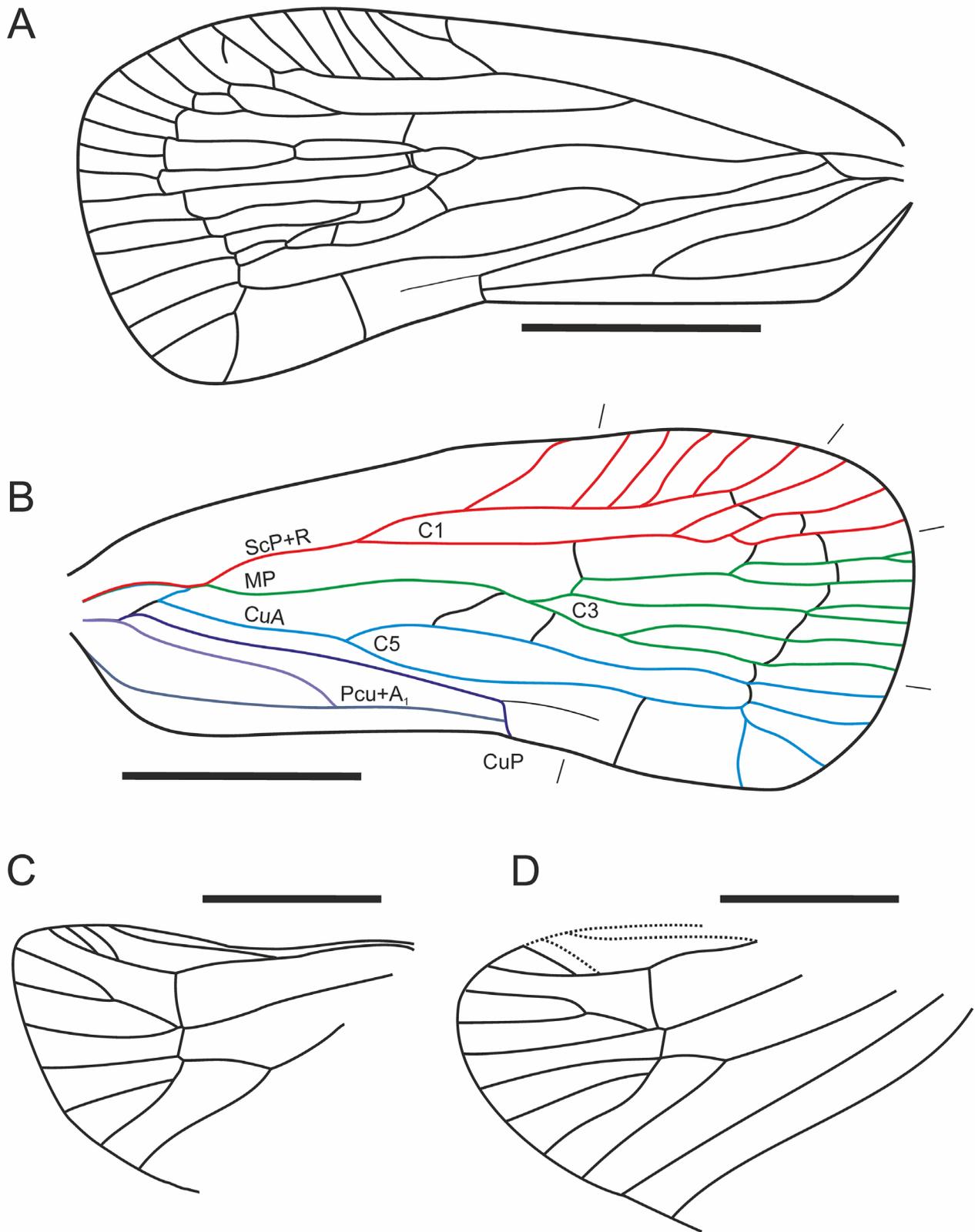


FIGURE 2. *Gedanochila museisucini* gen. et sp. nov. Holotype. A, left tegmen; B, right tegmen; C, right hind wing ventral view. D, left hind wing, dorsal view. Scale bar 2 mm



FIGURE 3. *Gedanochila museisucini* gen. et sp. nov. Holotype. A, General dorsal view; B, General ventral view. Scale bar: 2 mm.

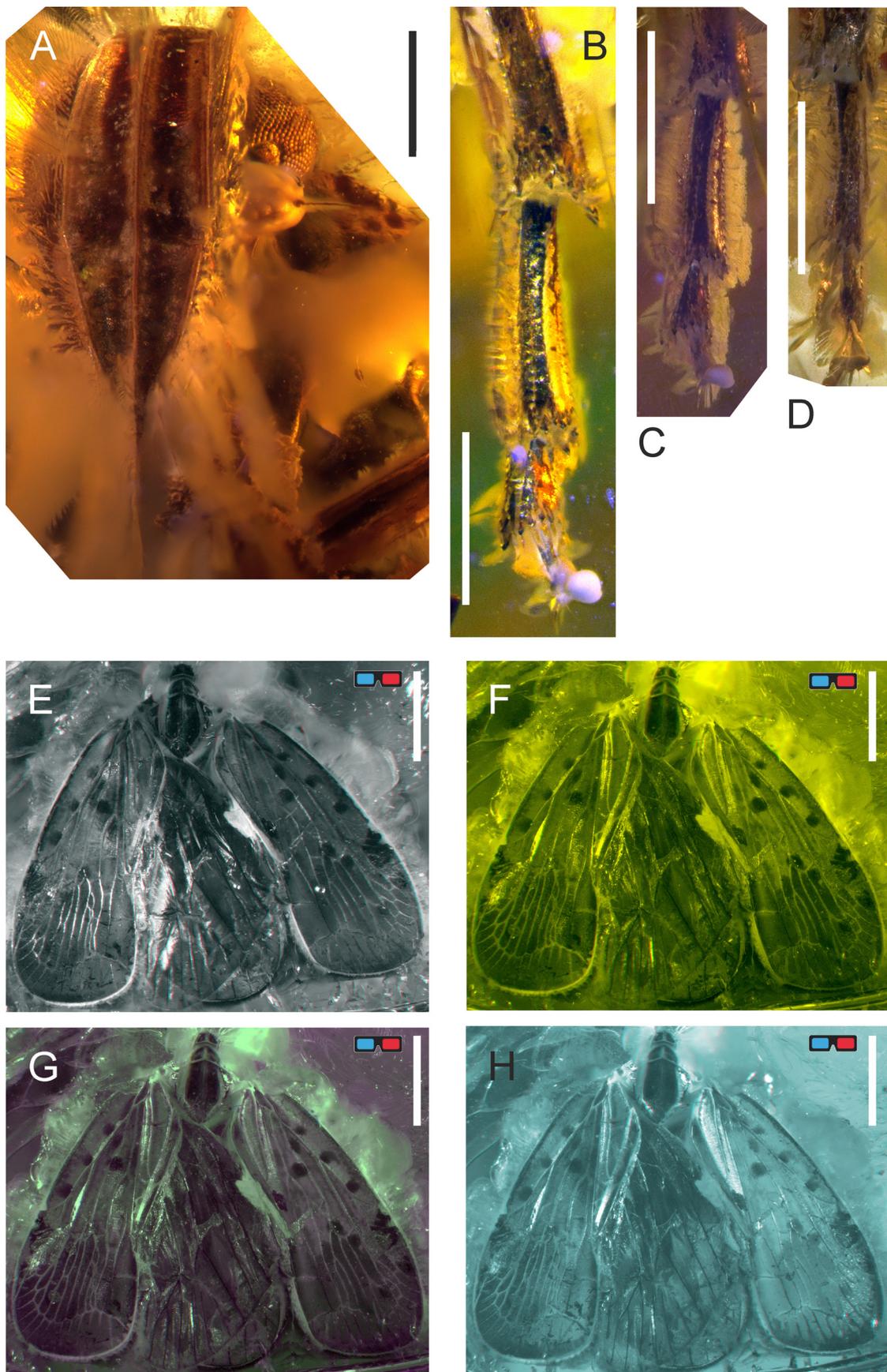


FIGURE 4. *Gedanochila museisucini* gen. et sp. nov. Holotype. A, Face; B, Apex of right metatibia and metatarsus; C, Right metatarsus; D, Left metatarsus; E-H, Anaglyph images of the specimen in dorsal view. Scale bars: 0.5 mm for A-D; 2 mm for E-H.

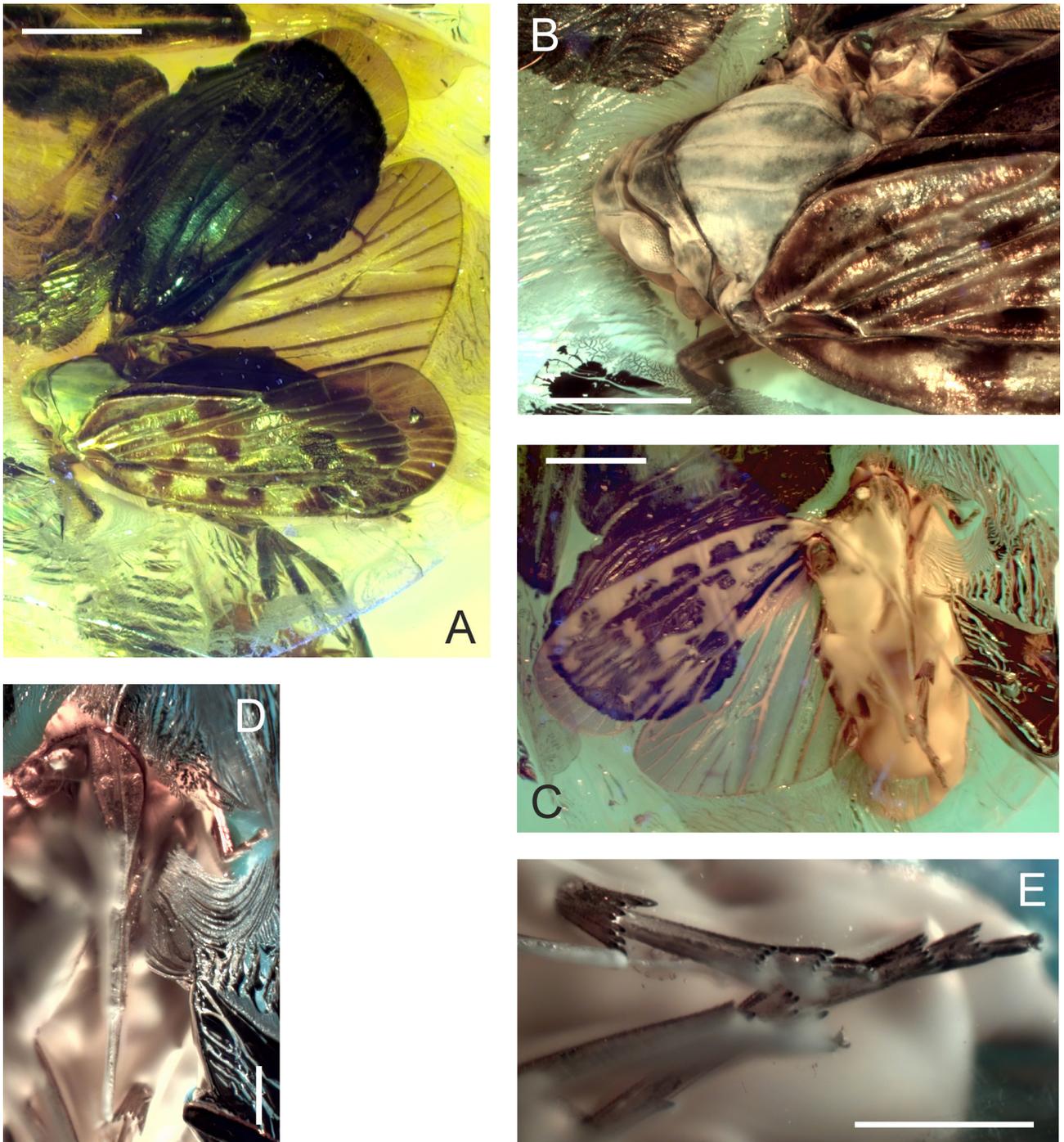


FIGURE 5. *Gedanochila museisucini* **gen. et sp. nov.** Paratype. A, General dorsal view. B, Anterior portion of body, laterodorsal view; C, Ventral view; D, Face and rostrum; E, Metatarsi. Scale bar 2 mm for A, C, 1 mm for B, D, E.

Discussion

The newly described genus *Gedanochila* **gen. nov.** fits quite well among other genera placed in Achilini, which is corroborated by the results of the analysis. However, its relationships with the other genera placed in the tribe need further investigation. *Gedanochila* **gen. nov.** clearly differs from the other extinct Achilini genera from Baltic amber, by the combination of characters of head capsule, pronotum and details of tegmen venation. In some respect, the tegmen of *Gedanochila* **gen. nov.** resembles that of *Protomenocria*, with clearly separated prenodal branch of ScP+RA, but clearly differs by presence of short common stalk of ScP+R+MP (present also in *Ouwea*, *Protepiptera*,

Angustachilus, *Cixidia* and *Achilus*). Slightly sigmoid stem MP in *Gedanochila* **gen. nov.** also resembles the pattern in *Ouwea*, but also in *Paratessum*. Other character similar in *Ouwea* and *Gedanochila* **gen. nov.** is the shape of cell C5 of the tegmen, with narrow section in the middle. In the genus *Psycheona* the basal portion of cell C5 is distinctly wider than the apical one, slightly similar pattern with wider basal section of cell C5 and narrowing apical section, as in *Gedanochila* **gen. nov.** and *Psycheona* is observed also in the genera *Angustachilus* and *Protoeiptera*, but no to such extent with narrower median portion or distinctly narrower apical section. Another character present in *Ouwea* and *Gedanochila* **gen. nov.**, but not in the other genera under consideration is short common stalk of CuA₂ branching on membrane, apical of apical line of veinlets. More basal fusion of claval veins Pcu and A₁ is also shared by *Ouwea* and *Gedanochila* **gen. nov.** Metathoracic wing, apart from not seen in *Gedanochila* **gen. nov.** anal area, is very similar to that of *Ouwea*, with 2 branches of RP, 3 terminals of MP (MP₃₊₄ not forked), four terminals of CuA.

Another point to notice, is presence of the small cells in *Gedanochila* **gen. nov.** left tegmen (not found on the right one), which may seem to be a developmental aberration. Interestingly similar small cells are present in the genus *Ouwea*, but such pattern has not been noted in any other recent taxa. This suggests, that this probably was caused by the same factors as other morphological abnormalities observed among the inclusions of the Eocene Achilidae taxa (Brysz & Szewo, data not published).

The Achilini Stål, 1866 as tribe was delimited based on presence of special anastomosis of anal veins of the hind wing (Emeljanov 1992), however such anastomosis is present also in Achillini Emeljanov, 1991, differing by shorter rostrum, not reaching metacoxae, with apical segment considerably shorter than wide and presence of narrow costal area in tegmen (Emeljanov 1991). Both tribes are now placed in subfamily Achilinae Stål, 1866 (Bartlett *et al.* 2018). The monophyly of Achilini is also supported also in our analysis by the elevation of posterior margin of vertex, the concave disc of vertex, and the elongate pedicel.

The subdivision of Achilini into three subtribes (Emeljanov 1992) is not strongly supported and seems to be artificial: Achilina Stål, 1866 was characterized by hind wings lacking median fold, branch A_{1a} diverging from stem considerably distad of connection with A₂ system of blind branches, with posterior branch of A₂ far from 2nd anal fold and presence of subapical setae on midmetarsomere; Cixidiina Emeljanov, 1992 was characterized by hind wing with median fold present, separation of A_{1a} at same level as connection with A₂ system of blind branches and presence of subapical setae on basi- and midmetarsomere; Elidipterina Fennah, 1950 was characterized by irregular venation of MP and CuA on membrane of tegmina, no blind branches in anal system of hind wings, with posterior branch of A₂ reaching margin at same place as 2nd anal fold (Fennah 1950, Emeljanov 1991, 1992). The analysis presented above suggests that the current subdivision of Achilini into subtribes should be discarded, and that only two lineages should be recognised. Interestingly, the genus *Paratessum* Emeljanov et Shcherbakov, 2009, places separately, although it was placed in Achilini on the distal forking of CuA₂ on membrane (Emeljanov & Shcherbakov 2009). What is interesting also is *Flatachilus* clearly separating from the other Achilini, by its tegmen venational characters.

Geographic distribution of Achilini as whole and taxa placed in Achilina is quite unusual. The genera *Achilus* and *Ouwea* are found in Australian region (in case of *Achilus* also in Novozelandic region), *Olmiana* is known only from Neotropical region—Argentina and Chile (Guglielmino *et al.* 2010, Campodonico 2017) and *Flatachilus* from Panamanian region - Pará, Brazil (Bourgoin 2021). While some of the records cannot be precisely placed, the known data point to relict environments, such as Kuranda forest in Australia for *Ouwea* (Distant 1907) or Lanín National Park in Argentina and Nahuelbuta National Park for *Olmiana* (Guglielmino *et al.* 2010, Campodonico 2017). Some of the insects were found associated with *Nothofagus* trees, which in general has a similar distribution with Achilina taxa, and is considered as a relic of Gondwana phytocenosis (van Steenis 1971, Knapp *et al.* 2005). However, such observations must be very carefully interpreted, as these ‘relic habitats’ have been shaped by many successive changes since the Gondwana.

The distributional pattern of the Recent taxa placed in Cixidiina appears at first glance simple—*Cixidia* (*Cixidia*) Fieber, 1866 is known from northern parts of the Palearctic, while species of *Cixidia* (*Eiptera*) Metcalf, 1922 are present in Palearctic, Nearctic and Saharo-Arabian regions. In addition, the only fossil placed to this subtribe—*Angustachilus* from the Eocene Baltic amber is known from Boreal region of the Eocene epoch (Fig. 6B). A more complex image is presented by Elidipterina genera: *Faventila* and *Paracatonidia* (Oriental), *Catonidia* (Oriental and Australian), *Booneta* (Oceanian region), *Uniptera* (Nearctic), *Elidiptera* (Nearctic and Panamanian), *Phradmonicus* and *Prinoessa* (Panamanian), *Messeis*, *Metaphradmon*, *Paraphradmon* and *Parelidiptera* (Neotropical).

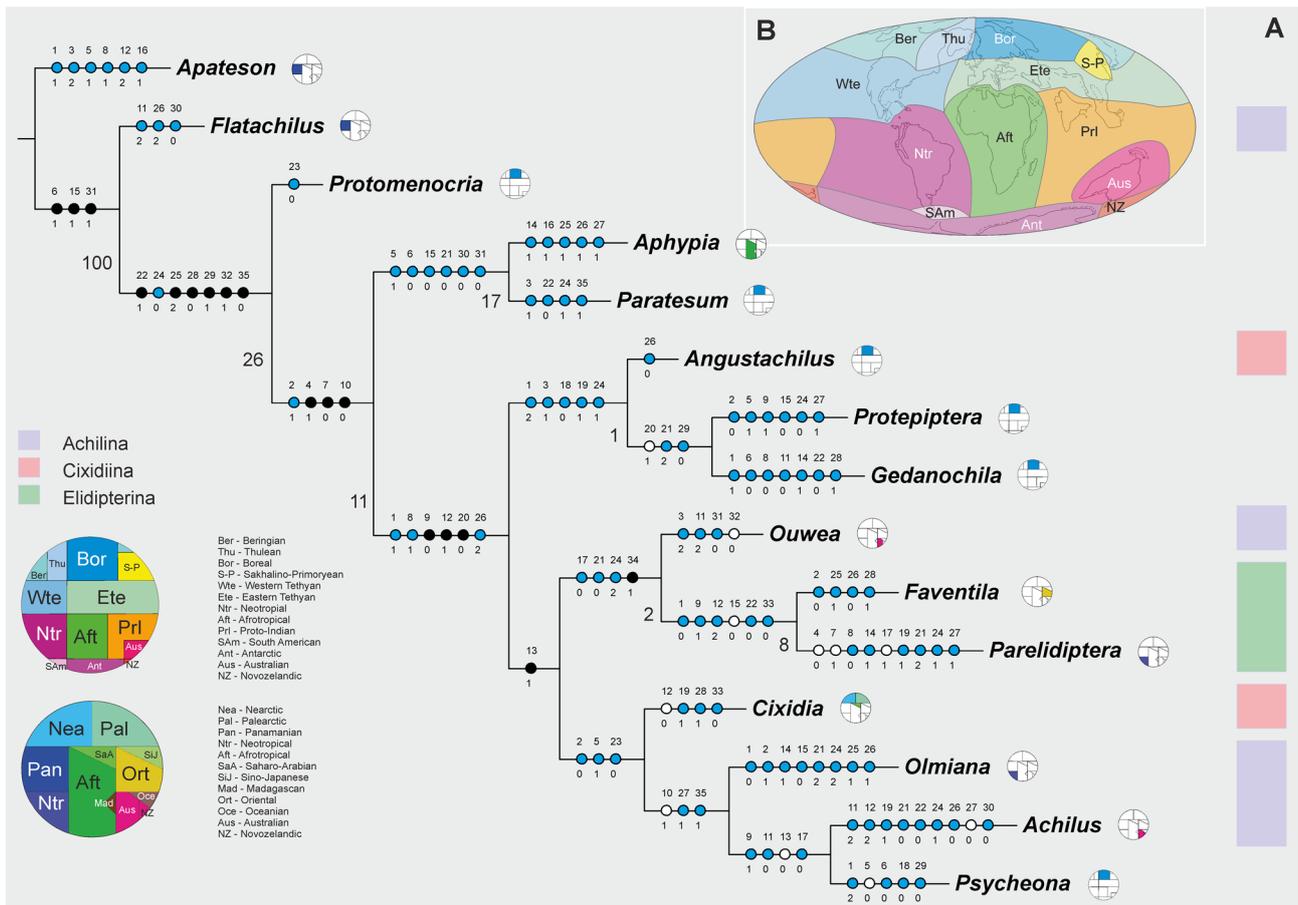


FIGURE 6. Grouping of the analyzed Achilini genera (New Technology Search algorithm, implied weighting, fast optimization). Apomorphies—black circles, plesiomorphies—white circles; homoplastic characters—blue circles. Bootstrap values at the nodes. Distribution of Recent taxa according to zoogeographical divisions of Holt *et al.* (2013), distribution of extinct taxa according to proposals of Meyen (1987) and Akhmet'ev (2004), modified.

Conclusion

For most Achilini the biological data are scarce and their ecological requirements and biological interactions remain very weakly known. Such disjunct and (probably) relictual distributions are confounding and inspiring. Distributional patterns of recent and extinct taxa provide valuable insight into the spatial history of life over both short and long periods of geological time. The incorporation of fossil data into estimates of ancestral distributions will not only improve the accuracy of those estimates but also provide additional temporal context (Barden & Ware 2017). Present-day distributions of organisms are the direct consequence of past instances of dispersal, vicariance, and extinction (Wiens & Donoghue 2004). A new fossil described above from inclusions in the Eocene Baltic amber allows to revisit the relationships of tribe Achilini and their past distribution, challenging its biogeographical pattern and its current classification.

Morphological characters of numerous Achilidae are still not sufficiently elaborated and recognized, as well as validity and importance of characters used for descriptions, identification and recognition of the groups. The knowledge of the recent taxa, their characters and morphological disparity, lack of modern studies and weak, insufficient descriptions influence the possibilities of reliable and full taxonomic and phylogenetic reconstructions. On the other hand, the long evolutionary history of the Achilini and Achilidae as whole and high rate of homoplastic characters observed among extinct and extant taxa is also very challenging in constructing the morphological matrices. Last, but not least, the lack of molecular background in reconstruction of relationships and phylogeny of Achilidae hampers the progress in research, testing and understanding of evolutionary traits and scenarios of the group.

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Authors' declarations

AMB designed the research, made the observations, documentation and illustrations, prepared draft and final manuscript; JS conducted the analysis of results and relationships, prepared the illustrations, prepared the draft and final manuscript; TB commented on the draft and final manuscript. Authors declare no conflict of interests.

References

- Agnarsson, I. & Miller, J.A. (2008) Is ACCTRAN better than DELTRAN? *Cladistics*, 24 (6), 1032–1038.
<https://doi.org/10.1111/j.1096-0031.2008.00229.x>
- Akhmet'ev, M.A. (2004) Klimat zemnogo shara v paleotsenie i eotsene po dannym paleobotaniki [Climate of the Earth in the Paleocene and Eocene: Implications of Paleobotany]. In: Semikhatov, M.A. & Chumakov, N.M. (Eds.), *Klimat v epokhi krupnykh biosferykh perestroek [Climate during Epochs of Great Biospheric Rearrangements]*. Nauka, Moscow, pp. 8–47. [in Russian]
- Akhmet'ev, M.A. & Zaporozhets, N.I. (2014) Sobytiya paleogena v Tsentralnoĭ Evrazii, ikh rol' v razvitiĭ flory i rastitel'nogo pokrova, smeshchenii granits fitkhorii i izmeneniyakh klimata. *Stratigrafiya. Geologicheskaya Korrelyatsiya*, 22 (3), 90–114. [published in English as: Akhmetiev, M.A. & Zaporozhets, N.I. (2014) Paleogene events in Central Eurasia: their role in the flora and vegetation cover evolution, migration of phytochore boundaries, and climate changes. *Stratigraphy and Geological Correlation*, 22 (3), 312–335]
<https://doi.org/10.1134/S0869593814030022>
- Amorim, D. de S. (1982) Classificação por seqüenciação: uma proposta para a denominação dos ramos retardados. *Revista brasileira de Zoologia*, 1 (1), 1–9.
<https://doi.org/10.1590/S0101-81751982000100001>
- Anufriev, G.A. & Emeljanov, A.F. (1988) Podotryad Cicadinea (Auchenorrhyncha)—tsikadovye. Suborder Cicadinea—(Auchenorrhyncha). In: Ler, P.A. (Ed.), *Opredelitel' nasekomykh Dal'nego Vostoka SSSR [Keys to the insects of the Far East of the USSR] Vol. 2*. Nauka, Leningrad, pp. 12–495 pp.
- Asche, M. (2015) The West Palaearctic Achilidae (Hemiptera, Fulgoromorpha: Fulgoroidea)—a review with description of five new species from the Mediterranean. *Nova Supplementa Entomologica*, 25, 1–135.
- Baatsen, M., von der Heydt, A.S., Huber, M., Kliphuis, M.A., Bijl, P.K., Sluijs, A. & Dijkstra, H.A. (2020) The middle to late Eocene greenhouse climate modelled using the CESM 1.0.5. *Climate of the Past*, 16, 2573–2597.
<https://doi.org/10.5194/cp-16-2573-2020>
- Ball, E.D. (1933) Some new Western leafhoppers of the fulgorid family Achilidae. *Pan-Pacific Entomologist*, 9, 133–138.
- Barden, P. & Ware, J.L. (2017) Relevant relicts: the impact of fossil distributions on biogeographic reconstruction. *Insect Systematics and Diversity*, 1 (1), 73–80.
<https://doi.org/10.1093/isd/ixx005>
- Bartlett, C.R., O'Brien, L.B. & Wilson, S.W. (2014) A review of the planthoppers (Hemiptera: Fulgoroidea) of the United States. *Memoirs of the American Entomological Society*, 50, 1–287. [<https://www.biodiversitylibrary.org/item/210531>]
- Bartlett, C.R., Deitz, L.L., Dmitriev, D.A., Sanborn, A.F., Soulier-Perkins, A. & Wallace, M.S. (2018) The diversity of the true hoppers (Hemiptera: Auchenorrhyncha) In: Footitt, R.G. & Adler, P.H. (Eds.), *Insect biodiversity. Science and society. Vol. 2*. Wiley-Blackwell, Oxford, pp. 501–590.
<https://doi.org/10.1002/9781118945582.ch19>
- Bourgoin, T. (1993) Female genitalia in Hemiptera Fulgoromorpha, morphological and phylogenetic data. *Annales de la Société Entomologique de France*, 29, 225–244.
- Bourgoin, T. (2022) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8. Updated 3 February 2022. Available from: <http://hemiptera-databases.org/flow/> (accessed 29 March 2022)

- Bourgoin, T., Wang, R.R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroiński, A., Yap, S. & Szwed, J. (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns of planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology*, 134 (1), 63–77.
<https://doi.org/10.1007/s00435-014-0243-6>
- Bourgoin, T., Wang, R.-R. & Gnezdilov, V.M. (2015) First fossil record of Caliscelidae (Hemiptera: Fulgoroidea): a new Early Miocene Dominican amber genus extends the distribution of Augilini to the Neotropics. *Journal of Systematic Palaeontology*, 14 (3), 211–218.
<https://doi.org/10.1080/14772019.2015.1032376>
- Brysz, A.M. & Szwed, J. (2018) The fossil record of the planthopper family Achilidae, with particular reference to those in Baltic amber (Hemiptera: Fulgoromorpha). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 107, 279–288.
<https://doi.org/10.1017/S175569101700041X>
- Brysz, A.M. & Szwed, J. (2019) Jeweled Achilidae—a new look at their systematics and relations with other Fulgoroidea (Hemiptera). *Monographs of the Upper Silesian Museum*, 10, 93–130.
<http://doi.org/10.5281/zenodo.3600279>
- Campodonico, J.F. (2017) Sobre la presencia de *Olmiana argentina* Guglielmino, Bückle y Emeljanov (Hemiptera: Fulgoroidea: Achilidae) en Chile. *Revista Chilena de Entomología*, 42, 23–24.
- Congreve, C.R. & Lamsdell, J.C. (2016) Implied weighting and its utility in palaeontological datasets: a study using modelled phylogenetic matrices. *Palaeontology*, 59, 447–465.
<https://doi.org/10.1111/pala.12236>
- de Bruyn, M., Stelbrink, B., Morley, R.J., Hall, R., Carvalho, G.R., Cannon, C.H., van den Bergh, G., Meijaard, E., Metcalfe, I., Boitani, L., Maiorano, L., Shoup, R. & von Rintelen, T. (2014) Borneo and Indochina are major evolutionary hotspots for Southeast Asian biodiversity. *Systematic Biology*, 63 (6), 879–901.
<https://doi.org/10.1093/sysbio/syu047>
- Distant, W.L. (1907) Rhynchotal notes xli. *Annals and Magazine of Natural History*, Series 7, 19, 277–295.
<https://doi.org/10.1080/00222930709487267>
- Distant, W.L. (1907) XXXIV.—Rhynchotal Notes.—XLI. *The Annals of Magazine of Natural History*, Series 7, 112, 277–295.
<https://doi.org/10.1080/00222930709487267>
- Emeljanov, A.F. (1990) Novy rod i triba semeštva Achilidae (Homoptera, Cicadina) iz baltiškogo yantarya [New genus and tribe of the family Achilidae (Homoptera, Cicadina) from the Baltic amber]. *Vestnik Zoologii*, 1, 6–10.
- Emeljanov, A.F. (1991) K voprosu ob obeme i podrazdeleniyakh sem. Achilidae (Homoptera, Cicadina). *Entomologicheskoe Obozrenie*, 70 (2), 373–93. [published in English as: Yemel'yanov, A.F. (1992) Toward the problem and limits and subdivisions of Achilidae (Homoptera, Cicadina). *Entomological Review*, 71 (1), 53–73]
- Emeljanov, A.F. (1992) Opisanie trib podsem. Achilinae (Homoptera, Achilidae) i utochnenie ikh sostava. *Entomologicheskoe Obozrenie*, 71 (3), 574–594. [published in English as: Yemel'yanov, A.F. (1993) Description of tribes of the subfamily Achilinae (Homoptera: Achilidae) and revision of their composition. *Entomological Review*, 72 (6), 7–27]
- Emeljanov, A.F. & Fletcher, M.J. (2004) *Hemielissum evansi*, a new genus and species of Breddiniolini (Hemiptera: Fulgoromorpha), being the first Australian record of the tribe, with a discussion of the taxonomic position of the Breddiniolini. *Australian Journal of Entomology*, 43, 38–42.
<https://doi.org/10.1111/j.1440-6055.2004.00403.x>
- Emeljanov, A.F. & Shcherbakov, D.E. (2009) New planthoppers of the tribe Achilini (Homoptera, Fulgoroidea, Achilidae) from Baltic amber. *Paleontological Journal*, 43 (9), 1008–1018.
<https://doi.org/10.1134/S0031030109090032>
- Emeljanov, A.F. & Shcherbakov, D.E. (2020) The first Mesozoic Derbidae (Homoptera, Fulgoroidea) from Cretaceous Burmese amber. *Russian Entomological Journal*, 29 (3), 237–246.
<https://doi.org/10.15298.rusentj.29.3.02>
- Evans, J.W. (1946) A natural classification of leaf-hoppers (Jassoidea, Hemiptera). Part 1. External morphology and systematic position. *Transactions of the Royal Entomological Society of London*, 96, 47–60.
<https://doi.org/10.1111/j.1365-2311.1946.tb00442.x>
- Fabricius, J.C. (1804) s.n. In: *Systema Piezatorum secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus*. C. Reichard, Brunswick, pp. i–xiv + 15–439 + 1–30.
<https://doi.org/10.5962/bhl.title.10490>
- Fennah, R.G. (1950) A generic revision of the Achilidae (Homoptera: Fulgoroidea) with descriptions of new species. *Bulletin of the British Museum (Natural History)*, Entomology, 1, 1–170.
<https://doi.org/10.5962/bhl.part.27228>
- Fieber, F.X. (1866) Neue Gattungen und Arten in Homoptera (Cicadina Bur.). *Verhandlungen der Kaiserlich-Königlichen Zoologisch-botanischen Gesellschaft in Wien*, 16, 497–516.
- Goloboff, P.A. & Catalano, S. (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32, 221–238.
<https://doi.org/10.1111/cla.12160>
- Goloboff, P.A., Farris, J. & Nixon, K. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.

<https://doi.org/10.1111/j.1096-0031.2008.00217.x>

- Goloboff, P.A., Torres, A. & Arias, J.S. (2018) Weighted parsimony outperforms other methods of phylogenetic inference under models appropriate for morphology. *Cladistics*, 34, 407–437.
<https://doi.org/10.1111/cla.12205>
- Gugliemino, A., Bückle, C. & Emeljanov, A.F. (2010) *Olmiana argentina*, a new genus and species of Achilidae (Hemiptera, Fulgoromorpha) from Argentina. *Zootaxa*, 2661 (1), 47–58.
<https://doi.org/10.11646/zootaxa.2661.1.3>
- Grimaldi, D.A. & Ross, A.J. (2017) Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. In: Fraser, N.C. & Sues, H.-D. (Eds.), *Terrestrial conservation Lagerstätten*. Dunedin Academic Press Ltd., Edinburgh, pp. 287–342.
- Hamilton, K.G.A. (1990) Chapter 6. Homoptera. In: Grimaldi, D.A. (Ed.), *Insects from the Santana Formation, lower Cretaceous, of Brazil*. *Bulletin of the American Museum of Natural History*, 195, 82–122.
- Haug, C., Mayer, G., Kutschera, V., Waloszek, D., Maas, A. & Haug, J.T. (2011) Imaging and documenting gammarideans. *International Journal of Zoology*, 2011 (380829), 1–9.
<https://doi.org/10.1155/2011/380829>
- Haug, J.T., Haug, C., Maas, A., Fayers, S.R., Trewin, N.H. & Waloszek, D. (2009) Simple 3D images from fossil and recent micromaterial using light microscopy. *Journal of microscopy*, 233 (1), 93–101.
<https://doi.org/10.1111/j.1365-2818.2008.03100.x>
- Herold, N., Buzan, J., Seton, M., Goldner, A., Green, J.A.M., Müller, R.D., Markwick, P. & Huber, M. (2014) A suite of early Eocene (~ 55 Ma) climate model boundary conditions, *Geoscientific Model Development*, 7, 2077–2090.
<https://doi.org/10.5194/gmd-7-2077-2014>, 2014
- Herrera-Flórez, A.F., Braig, F., Haug, C., Neumann, C., Wunderlich, J., Hörnig, M.K. & Haug, J.T. (2020) Identifying the oldest larva of a myrmeleontiformian lacewing—a morphometric approach. *Acta Palaeontologica Polonica*, 65 (2), 235–250.
<https://doi.org/10.4202/app.00662.2019>
- Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P. H., Graham, C.H., Graves, G.R., Jönsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbek, C. (2013) An update of Wallace’s zoogeographic regions of the world. *Science*, 339 (6115), 74–78.
<https://doi.org/10.1126/science.1228282>
- Hörnig, M.K., Sombke, A., Haug, C., Harzsch, S. & Haug, J.T. (2016) What nymphal morphology can tell us about parental investment—a group of cockroach hatchlings in Baltic amber documented by a multi-method approach. *Palaeontologia Electronica*, 19.1.6A, 1–20.
<https://doi.org/10.26879/571>
- Kirby, W. (1819) XXVIII. A description of several new species of insects collected in New Holland by Robert Brown, Esq. F.R.S. Lib. Linn. Soc. *Transactions of the Linnean Society of London*, 12-2, 454–482.
<https://doi.org/10.1111/j.1095-8339.1817.tb00240.x>
- Knapp, M., Stöckler, K., Havell, D., Delsuc, F., Sebastiani, F. & Lockhart, P.J. (2005) Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (Southern Beech). *PLOS Biology*, 3, 38–43.
<https://doi.org/10.1371/journal.pbio.0030014>
- Kosmowska-Ceranowicz, B. (2017) *Amber in Poland and in the World. Second Edition, Revised*. Wydawnictwa Uniwersytetu Warszawskiego, Warsaw, 310 pp.
- Latreille, P.A. (1807) *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Vol. 3*. Amand Koenig bibliopolam, Parisiis et Argentorati, 258 pp.
<https://doi.org/10.5962/bhl.title.65741>
- Lefebvre, F., Bourgoin, T. & Nel, A. (2007) New Cixiidae and Achilidae fossils from Middle Eocene Baltic amber (Hemiptera: Fulgoromorpha). *Annales de la Société Entomologique de France*, 43 (1), 37–43.
<https://doi.org/10.1080/00379271.2007.10697491>
- Liang, A.-P. (2001) Morphology of antennal sensilla in *Achilixius sandakanensis* Muir (Hemiptera: Fulgoromorpha: Achilixiidae) with comments on the phylogenetic position of the Achilixiidae. *The Raffles Bulletin of Zoology*, 49, 221–225. [<https://lknhm.nus.edu.sg/app/uploads/2017/04/49rbz221-225.pdf>]
<https://doi.org/10.1055/s-2001-16113>
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio Decima, reformata*. Laurentii Salvii, Holmiae, 824 pp.
<https://doi.org/10.5962/bhl.title.542>
- Long, J.K., Yang, L. & Chen, X.S. (2015) A review of Chinese tribe Achilini (Hemiptera: Fulgoromorpha: Achilidae), with descriptions of *Paracatonidia webbeda* gen. & sp. nov. *Zootaxa*, 4052 (2), 180–186.
<https://doi.org/10.11646/zootaxa.4052.2.2>
- Maddison, W.P. & Maddison, D.R. (2019) Mesquite: a modular system for evolutionary analysis. Version 3.61. Build 927. 26 December 2019. Available from: <http://mesquiteproject.org> (accessed 29 March 2022)
- Melichar, L. (1908) Nové rody a druhy Homopter z východní Afriky. *Časopis České Společnosti Entomologické*, 5, 1–15.
- Metcalf, Z.P. (1938) The Fulgorina of Barro Colorado and other parts of Panama. *Bulletin of the Museum of Comparative Zoology*, 82, 277–423, pls 1–23. [<https://www.biodiversitylibrary.org/page/4773238>]

- Metcalf, Z.P. (1948) *General Catalogue of the Hemiptera. Fascicle IV. Fulgoroidea. Part 10 Achilidae*. Smith College, Northampton, Massachusetts, 85 pp.
- Meyen, S.V. (1987) *Osnovy paleobotaniki*. Nedra, Moskva, 403 pp. Published in English as Meyen, S.V. (1987) *Fundamentals of palaeobotany*. Chapman & Hall, London and New York, xxi + 432 pp.
<https://doi.org/10.1007/978-94-009-3151-0>
- Muir, F. (1923) *Achilixius*, a new genus, constituting a new family of the Fulgoroidea (Homoptera). *Philippine Journal of Science*, 22, 483–487.
- Nixon, K.C. (2002) WinClada. Version 1.00.08. Published by the author, Ithaca, New York.
- Nixon, K.C. (2004) ASADO. Version 1.61. TNT-MrBayes Slaver (v1 5.30). Published by the author, Ithaca, New York. [program]
- O'Brien, L.B. (1971) Systematics of the tribe Plectoderini (Insecta, Fulgoroidea, Achilidae) in America North of Mexico. *University of California Publications in Entomology*, 64, 1–79.
- Sadowski, E.-M., Schmidt, A.R. & Denk, T. (2020) Staminate inflorescences with in situ pollen from Eocene Baltic amber reveal high diversity in Fagaceae (oak family). *Willdenowia*, 50, 405–517.
<https://doi.org/10.3372/wi.50.50303>
- Sadowski, E.-M., Schmidt, A.R., Seyfullah, L. & Kunzmann, L. (2017) Conifers of the 'Baltic amber forest' and their palaeoecological significance. *Stapfia*, 106, 1–73.
- Savazzi, E. (2011) *Digital photography for science. Close-up photography, macrophotography and photomacrography*. Lulu Press, Inc., Morrisville, North Carolina, 698 pp.
- Spinola, M. (1839) Essai sur les Fulgorelles, sous-tribu de la tribu des Cicadaïes, ordre des Rhyngotes. (Suite). *Annales de la Société Entomologique de France*, 8, 339–454. [<https://www.biodiversitylibrary.org/page/33710252>]
- Stål, C. (1862) Bidrag till Rio de Janeiro-tratzens Hemipter-fauna. II. *Kungliga Svenska vetenskapsakademien Handlingar*, 3 (6), 1–75. [<https://www.biodiversitylibrary.org/page/2566801>]
- Stål, C. (1866) Hemiptera Homoptera Latr. *Hemiptera Africana*, 4, 1–276. [<https://www.biodiversitylibrary.org/item/35350>]
- Swezey, O.H. (1904) A preliminary catalogue of the described species of the family Fulgoridae of North America, North of Mexico. *Bulletin. Ohio Department of Agriculture. Division of Nursery and Orchard Inspection*, 3, 1–48.
- Szwedo, J. (2006) A new genus *Waghilde* gen. nov. representing a new tribe of the planthopper family Achilidae from the Eocene Baltic amber (Hemiptera: Fulgoromorpha). *Annales Zoologici*, 56 (1), 167–174.
- Szwedo, J. (2008) Achilidae from the Eocene Baltic amber. *Bulletin of Insectology*, 61 (1), 109–110.
- Szwedo, J. (2018) The unity, diversity and conformity of bugs (Hemiptera) through time. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 107 (2–3), 109–128.
<https://doi.org/10.1017/S175569101700038X>
- Szwedo, J., Bourgoïn, T. & Lefebvre, F. (2004) *Fossil planthoppers (Hemiptera Fulgoromorpha) of the world. An annotated catalogue with notes on Hemiptera classification*. Studio 1, Warsaw, 208 pp.
- Szwedo, J. & Drohojowska, J. (2016) A swarm of whiteflies—the first record of gregarious behavior from Eocene Baltic amber. *The Science of Nature*, 103 (35), 1–6 + 1–26.
<https://doi.org/10.1007/s00114-016-1359-y>
- Uhler, P.R. (1896) Summary of the Hemiptera of Japan presented to the United States National Museum by Professor Mitzukuri. *Proceedings of the United States National Museum*, 19, 255–297.
<https://doi.org/10.5479/si.00963801.1108.255>
- Urban, J.M. & Cryan, J.R. (2007) Evolution of the planthoppers (Insecta: Hemiptera: Fulgoroidea). *Molecular Phylogenetics and Evolution*, 42, 556–772.
<https://doi.org/10.1016/j.ympev.2006.08.009>
- Usinger, R.L. (1939) *Protepiptera*, a new genus of Achilidae from Baltic amber (Hemiptera, Fulgoroidea). *Psyche*, 46, 65–67.
<https://doi.org/10.1155/1939/43827>
- van Steenis, C.G.G.J. (1971) *Nothofagus*, key genus of plant geography, in time and space, living and fossil, ecology and phylogeny. *Blumea—Biodiversity, Evolution and Biogeography of Plants*, 19, 65–98.
- Walker, F. (1858) Homoptera. *Insecta saundersiana: or characters of undescribed insects in the collection of William Wilson Saunders*. John Van Voorst, London, 117 pp.
<https://doi.org/10.5962/bhl.title.5112>
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, 19 (12), 639–644.
<https://doi.org/10.1016/j.tree.2004.09.011>
- Wilson, S.W., Mitter, C., Denno, R.F. & Wilson, M.R. (1994) Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. In: Denno, R.F. & Perfect, T.J. (Eds.), *Planthoppers: Their Ecology and Management*. Chapman & Hall, New York, pp. 7–113.
https://doi.org/10.1007/978-1-4615-2395-6_2
- Wolfé, A.P., McKellar, R.C., Tappert, R., Sodhi, R.N.S. & Muehlenbachs, K. (2016) Bitterfeld amber is not Baltic amber: Three geochemical tests and further constraints on the botanical affinities of succinite. *Review of Palaeobotany and Palynology*, 225, 21–32.
<https://doi.org/10.1016/j.revpalbo.2015.11.002>