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A NEW GENUS *WAGHILDE* GEN. NOV. REPRESENTING A NEW TRIBE OF THE PLANTHOPPER FAMILY ACHILIDAE FROM THE EOCENE BALTIC AMBER (HEMIPTERA: FULGOROMORPHA)

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Abstract.— A new genus and species of extinct Achilidae — *Waghilde baltica* **gen.** and **sp. nov.**, from the Eocene Baltic amber is described. It represents a new tribe of Achilinae - Waghildini **trib. nov.** The relationships of Waghildini and its placement among recently recognized tribes of Achilinae is discussed.

Key words.— Achilidae, Waghildini, new tribe, *Waghilde*, new genus, *Waghilde baltica*, new species, Eocene, Baltic amber, fossils, classification, phylogeny

INTRODUCTION

The family Achilidae is one of the old families lying near the basal stock of recent Fulgoroidea (Hemiptera: Fulgoromorpha), but with still unresolved taxonomic problems. Extant Achilidae are distributed worldwide, and reach far North to the cold regions of the temperate zone in North Europe. Imagines of Achilidae are primarily associated with dicotyledones; however, achilids seem to be more closely associated with gymnosperms than any other fulgoroid family. The majority of species as imagines are polyphagous, but many achilids are known from a single plant family (Wilson et al. 1994).

About 150 genera and 450 species of Achilidae have been described so far, comprised in three subfamilies: Bebaiotinae, Achilixinae and Achilinae. The status of the two former groups is still debatable; they used to be treated as representatives of a distinct family - Achilixiidae, (Wilson 1989) or believed to be separate subfamilies, as stated by Emeljanov (1991), or moved to Cixiidae, as believed by Liang (2002). On the other hand, some taxa placed in the family Derbidae - highly differentiated family regarded as a sister group of Achilidae - share characters with Achilidae, and also some Achilidae are known for derbid-like characters. Classification of the Achilidae has been reviewed by Fennah (1950). Later, classification was elaborated by Emeljanov (1991, 1992, 2005) and Emeljanov and Fletcher (2004). The most recent scheme of subdivisions of Achilinae is presented in Table 1.

The placement of the extinct tribe Ptychoptilini Emeljanov, 1990, described from the Eocene Baltic amber (Emeljanov 1990, Szwedo and Stroiński 2001) remains unresolved. Representatives of Ptychoptilini are highly derivative, and shares some of features with basal tribes of Derbidae: Ipsnolini and Vinatini.

The fossil record of Achilidae can be traced back to the Lower Cretaceous (Szwedo et al. 2004). These fossils, 120 million years old, are named *Acixiites immodesta* Hamilton, 1990 and *Acixiites costalis* Hamilton, 1990. In the Upper Cretaceous, Turonian-Cenomanian amber of Myanmar (Burma) a single species - *Niryasaburnia burmitina* (Cockerell, 1917) is formally described, but cannot be placed among recently recognized tribes of Achilidae (Szwedo 2004a). Achilidae are quite numerous among Eocene, Lutetian Baltic amber inclusions (Szwedo et al. 2004). From the Eocene/Oligocene strata of Gurnet Bay, Isle of Wight, another species *Hooleya indecisa* Cockerell, 1922 is recorded, placed in tribe Achillini (Emeljanov 1994). Another species described from imprints is a specimen named *Elidiptera regularis* Scudder, 1890 from Eocene deposits of Florissant,

Table 1. Scheme of subdivisions of Achilinae.

subfamily	supertribe	tribe	subtribe
Achilinae	Myconites Fennah, 1950	Myconini Fennah, 1950	
		Rhotalini Fennah, 1950	
		Mycarini Emeljanov, 1991	
		Amphignomini Emeljanov, 1991	
		Plectoderini Fennah, 1950	
	Achilites Stål, 1866	Achilini Stål, 1866	Elidipterina Fennah, 1950
			Achilina Stål, 1866
			Cixidiina Emeljanov, 1991
		Achillini Emeljanov, 1991	
	Apatesonites Metcalf, 1938	Ilvini Emeljanov, 1991	
		Seviini Emeljanov, 1991	
		Apatesonini Metcalf, 1938	
		Tropiphlepsiini Emeljanov, 1991	
	not placed	Ptychoptilini Emeljanov, 1990	
		Waghildini Szwedo, 2006	

Colorado, U.S.A. The taxonomic position of this species is uncertain and needs revision and reconsideration. Undescribed Achilidae are known from the Palaeocene of Denmark, the Lowermost Eocene of France, and the Oligocene/Miocene of Dominican Republic.

SYSTEMATIC PALAEONTOLOGY

Order **Hemiptera** Linnaeus, 1758

Suborder **Fulgoromorpha** Evans, 1946

Superfamily **Fulgoroidea** Kirkaldy, 1907

Family **Achilidae** Stål, 1866

Subfamily **Achilinae** Stål, 1866

Waghildini trib. nov.

Type genus. *Waghilde* gen. nov.

Diagnosis. In general appearance similar to Rhotalini, but clearly differing in tegminal venation pattern. Tegmen with vein CuA forked once in prenodal region, as in other Achilinae tribes (CuA three-branched in prenodal region in Rhotalini); posterior branch of CuA with a few terminals (in Rhotalini posterior branch of CuA anastomosed with marginal vein with numerous terminals). Wing with median fold between veins M and CuA reaching to margin of wing. Lateral carinae of frons not widened or forming narrow concavities of lateral field of frons (lateral and intermediate carinae of frons fused, widened or forming narrow concavities in Rhotalini). Hind tibia flattened, with 6–8 lateral spines (hind tibia not flattened, with 5–7 lateral spines in Rhotalini) and 8–9 apical teeth not arranged in regular row and different in size (5–6 apical teeth of similar size arranged in row in Rhotalini). Apical teeth of first and second hind tarsomere with thick subapical setae, with exception of external ones (only internal teeth of hind leg mid tarsomere with long subapical setae in Rhotalini). Abdomen with trichobothria.

Waghilde gen. nov.

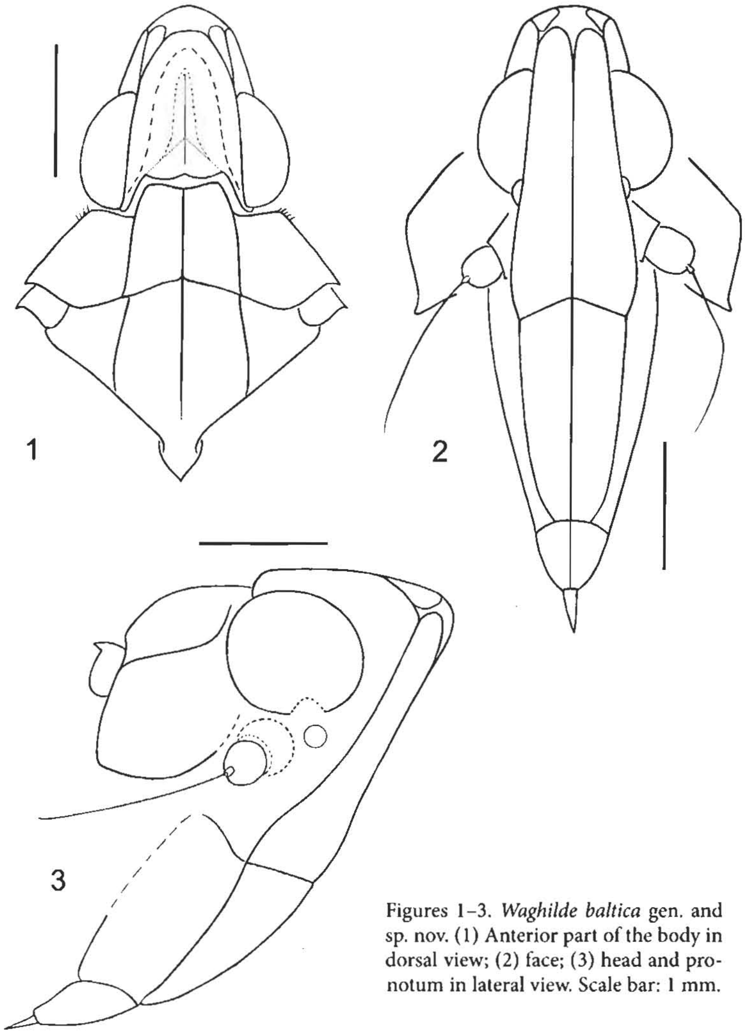
Type species. *Waghilde baltica* sp. nov.

Etymology. Waghilde – name of the water lady (mermaid) of the Baltic Sea in the German mythology. Gender: feminine.

Age and occurrence. Eocene, Lutetian, ca. 43.5 Ma; Baltic amber, coast of Baltic Sea.

Diagnosis. Differs from the extant genera of Rhotalini by the head distinctly longer than pronotum, apical callosity of head wider than long, distinct trigons, lateral margins of vertex elevated, posterior margin of vertex not strongly shifted anteriad, disc of vertex triangularly elevated at posterior margin. Venation distinct, veinlet *icu* reaching margin distinctly anteriad from the posterior system of CuA branching, as in most Achilinae (in Rhotalini this veinlet is close to the forking system of posterior branch of CuA). Clavus long, exceeding half of tegminal length, claval veins junction at ⅔ of claval length. Hind tibiae flattened, with more than 6–8 lateral spines, and 8–9 distinct apical teeth. Abdominal trichobothria arranged in rows, with long setae. Ovipositor short, of raking up-kneading type.

Description. Vertex in mid line about 1.8 times as long as pronotum in mid line. Vertex about 1.5 times as long in mid line as wide at posterior margin; lateral margins of vertex subparallel, then converging anteriad from the level of anterior border of compound eyes; posterior margin of vertex almost straight. Frons narrow with distinct median carina on all its length, frons about twice as long as wide at widest point, at level of antennae. Lateral carinae of frons not widened or forming narrow concavities of lateral field of frons. Clypeus about as long as frons. Rostrum slightly exceeding hind coxae. Pronotum wider than head with compound eyes, with distinct and elevated median disc; anterior margin of disc almost straight, posterior margin of pronotum shallowly excavated; median and lateral carinae of disc and lateral carinae distinct. Mesonotum shorter than wide, with median and lateral carinae distinct. Tegmen fully developed, with anterior margin distinctly convex at base, then almost straight, posterior margin widely rounded; apex of clavus slightly exceeding half of tegminal length. Venation distinct, veinlet *icu* reaching margin shifted distinctly anteriad from the posterior system of CuA branching. Hind wings fully developed. Hind tibia flattened, with distinct lateral spines, apical teeth not arranged in regular row, hind tarsus with basitarsomere and mid tarsomere with subapical setae on teeth



Figures 1–3. *Waghilde baltica* gen. and sp. nov. (1) Anterior part of the body in dorsal view; (2) face; (3) head and pronotum in lateral view. Scale bar: 1 mm.

with exception of external ones. Ovipositor short, of making up-kneading type.

Waghilde baltica sp. nov.
(Figs 1–13 and 15–27)

Etymology. Species name refers to Baltic Sea (Mare Balticum).

Diagnosis. Vertex with disc shallowly excavated, posterior portion reaching posterior border with triangular elevation. Clypeus strongly convex. Median disc of pronotum 1.2 times wider at posterior border than long in mid line. RA with 4 terminals, RP with 3 terminals M with 5 terminals, posterior branching system of CuA with 4 terminals. First branching of Sc+R at ¼ of tegmen length, first branching of M at level of nodal line, first branching of CuA at level of claval veins Pcu and A_1 junction. Clavus long, exceeding half of tegminal length, claval veins junction at ⅔ of clavus length. Hind tibiae flattened, with 6–8 lateral spines and 8–9 apical teeth. Hind basitarsomere with row of 6–7 apical teeth, with subapical setae wit exception of external teeth, mid tarsomere of hind leg with row of 8–9 apical teeth with subapical setae, with exception of external teeth.

Description. Total length 11.1 mm. Length of body 7.7 mm. General coloration dark brown.

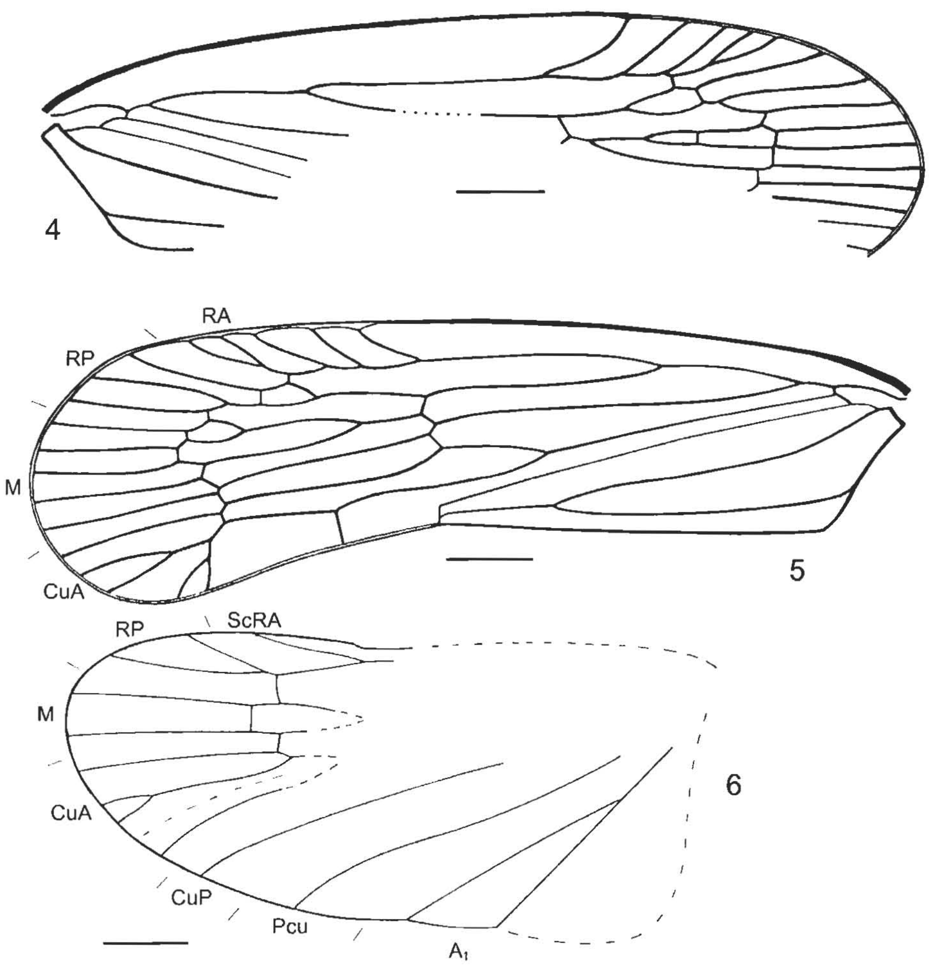
Head with compound eyes narrower (1.56 mm) than pronotum (2.4 mm). Vertex distinctly longer (1.22 mm) than wide (0.82 mm), anterior margin short, lateral margins subparallel, converging anteriad slightly anteriorly of anterior angle of compound eyes, posterior margin shallowly excavate, nearly straight. Disc of vertex shallowly concave, posterior portion with triangular elevation, without median carina. Trigons distinct. Anterior callosity wider than long. Frons narrow, 1.9 mm long in mid line, slightly longer at lateral line, 0.92 mm wide at widest point at level of antennae; lateral margins subparallel in upper portion then diverging almost to the level of clypeal suture. Lateral carinae of frons not widened or forming narrow concavities of lateral field of frons, median carina distinct, complete, disc of frons concave. Frontoclypeal suture slightly arcuate. Clypeus distinctly convex, about as long as frons (2 mm), lateral carinae distinct, converging downwards, median carina present. Clypellus short and narrow. Rostrum 3.2 m long, slightly exceeding hind coxae; subapical segment longer (1.72 mm) than apical segment (1.32 mm). Circumocular portion of head capsule shallowly concave. Compound eyes round. Antenna with distinct antafossa, second segment elongately oval, about ⅔ as wide as long, arista 1.5 mm long. Lateral ocelli distinct.

Pronotum 0.68 mm long in mid line, 2.4 mm wide. Median portion (disc) elevated delimited by lateral carinae of disc, median carina distinct. Anterior border of disc straight. Lateral portion of pronotum sloping downwards, concave, delimited by distinct lateral carina. Postocular field of pronotum with lower margin straight, not emarginated. Anterolateral angles with group of short and stout setae. Posterior margin of pronotum shallowly excavate.

Tegulae about twice as wide as long, without carinae.

Mesonotum with disc flat, delimited by lateral carinae, median carina distinct, lateral portions sloping downwards, posterior portion slightly elongated and widened, emarginate.

Tegmen 8.8 mm long, about 4 times as long as wide. Anterior margin distinctly curved at base then almost straight, posterior margin widely rounded. Clavus with apex exceeding half of tegmen length, posterior portion of tegmen (membrane) widened. Costal complex of



Figures 4–6. *Waghilde baltica* gen. and sp. nov. (4) Right tegmen (visible portion); (5) left tegmen; (6) left wing (visible portion). Scale bar: 1 mm.

veins slightly widened at base, with basicostal field not distinctly widened. Basal cell elongate. Common stem of Sc+R+M very short. Sc+R forked distinctly anteriad of claval veins junction, $ScRA_1$ forked at level of claval apex, RA with 4 terminals; RP forked at level of *icu* veinlet reaching tegmen margin, with 3 terminals. Vein M forked at level of claval apex, with 5 terminals. Vein CuA forked at level of claval veins junction, anterior branch with single terminal, posterior branch forming branching system at level of apical veinlets, reaching margin. First veinlets *r-m* and *m-cu* at level of first M branching; apical veinlets: *ir*, *im*, *m-cu* and *icu* not forming distinct apical line. Veinlet *icu* reaching margin, distinctly shifted anteriad from the posterior system of CuA branching.

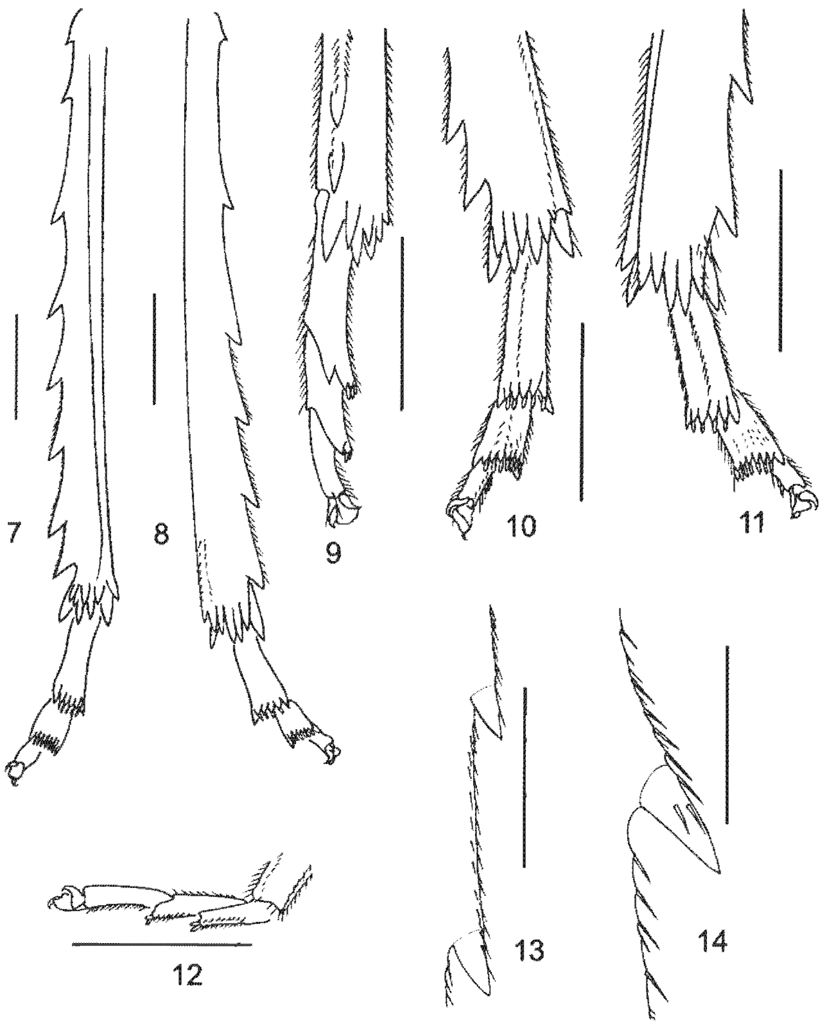
Wing fully developed, hyaline. Vein $ScRA_1$ reaching margin at level of RP forking, vein RP with two terminals, vein M with two terminals, vein CuA with 4 terminals, veins CuP and Pcu single, vein A_1 forked at about ½ of its length. Ano-jugal portion of wing not visible. Veinlet *r-m* long, at level of RP forking, veinlet *im* present, anteriad of veinlet *r-m*, veinlet *m-cu* at same level as veinlet *r-m*. Cubital fold reaching margin of wing.

Fore and mid legs slender, fore femur slightly shorter than fore tibia, mid femur slightly shorter than mid tibia. Fore and mid femora quadrangular in cross section, margins provided with rows of short, delicate setae. Tarsomeres of fore and mid legs of similar length, tarsal claws and arolium distinct. Basitarsomere and mid tarsomere of fore and mid legs provided with two stout apical platellae. Hind coxa big, conical with distinct meracanthus. Hind femur 2.15 mm long, hind tibia 5.1 mm long, slightly flattened, with distinct lateral spines. Left hind tibia with 6 lateral spines and row of 8 apical teeth, right tibia with 8 lateral spines and row of 9 apical teeth. Tarsus 1.8 mm long; basitarsomere longer than combined length of mid and apical tarsomeres. Basitarsomere 1.17 mm long, left with row of 6 apical teeth, right with row of 7 apical teeth; subapical setae present with exception of external teeth. Mid tarsomere 0.77 mm long, with row of apical teeth, left with 8 teeth, right with 9 teeth, subapical setae present with exception of external teeth. Apical tarsomere shorter than subapical one, tarsal claws distinct, arolium triangular, wide.

Abdomen about as long as wide (3.16 mm), abdominal sternites IV–VI with rows of trichobothria, female subgenital sternite with group of trichobothria (?). Ovipositor short, gonapophysis VIII short, subtriangular with tumid apex, teeth not visible.

Material. Holotype, female. Eocene Baltic amber. collection of Jacek Serafin AUF 061JS, MNHN-LP-R 63856 deposited in the Département Systématique et Evolution, Museum National d'Histoire Naturelle, Paris.

Preservation. Ventral part of body partly covered with milky veil. Left fore leg and mid leg missing. Details of face, lateral portion of head capsule, bases of antennae, lateral portion of thorax, bases of legs, ventral portion of abdomen and genital structures weakly visible because of milky veil.



Figures 7–14. *Waghilde baltica* gen. and sp. nov. (7) Right hind tibia and tarsus; (8) left hind tibia and tarsus; (9) right tarsus in lateral view; (10) right hind tarsus; (11) left hind tarsus; (12) left fore tarsus; (13) lateral spine of hind tibia. (14) *Hebrotasa madagascariensis* Emeljanov, 2005. Lateral spine of hind tibia. Scale bar: 1 mm for 7–12, 0.5 mm for 13 and

Discussion

Waghildini in external appearance superficially resembles Rhotalini, particularly because of the elongate head and hind tibia with lateral spines, but differs in numerous details of structure. Regarding head capsule structure, forms with protruding head are known in various tribes of Achilinae. However, distinct areolets (trigons) are not known among Rhotalini, but recorded among Achilini. The callose margin between vertex and frons is similar to that present in Rhotalini, but such callosity is present also in some Achilini. Regarding structure of the frons and clypeus, Waghildini are similar to representatives of Myconini and Rhotalini, with distinct median carina and lateral carinae of postclypeus not continuing on anteclypeus. In respects to the lateral carinae of pronotum, Waghildini differs from Myconini by only single lateral carina of pronotum as in Rhotalini. Regarding the venation of tegmen Waghildini are similar to Achilini: Cixidiina, but the forking of stem Sc+R is distinctly more anteriad than in Achilini: Cixidiina, resembling the pattern found in Mycarini. Waghildini differs from Myconini, Rhotalini and Achilini: Cixidiina in the pattern of branching of vein M of tegmen. Stem M_{3+4} in Waghildini is branched distinctly more apicad than in Achilini: Cixidiina, at apical line of veinlets. Pattern of branching of vein CuA differs distinctly from both Rhotalini and Myconini (vein CuA polymerized in those tribes), resembling those of Achilini: Cixidiina. Wing venation of Waghildini seems to be similar to Mycarini and Achilini: Cixidiina, particularly in scarce bifurcation of veins Sc+R and M, and long veinlet *r-m*. Unfortunately, the ano-jugal lobe is not visible, and the venation of this crucial portion of wing is not available for study. The posterior branch of vein CuA and CuP in Waghildini are approximated, but not in such extent as in Rhotalini. In Waghildini the veinlet *im* is present which is an exceptional feature, not found in Myconini or Achilini. The wing with a row of apical veinlets is present only in Rhotalini, but in this case the veinlets are distinctly more apicad and numerous than in Waghildini. In Waghildini the cubital fold seems to reach margin of wing as in Rhotalini. Waghildini and Rhotalini

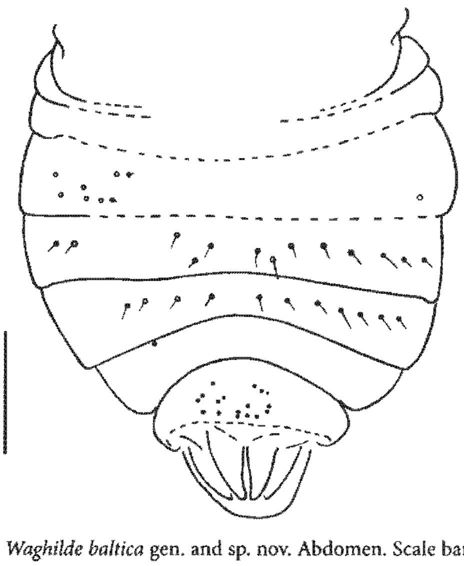
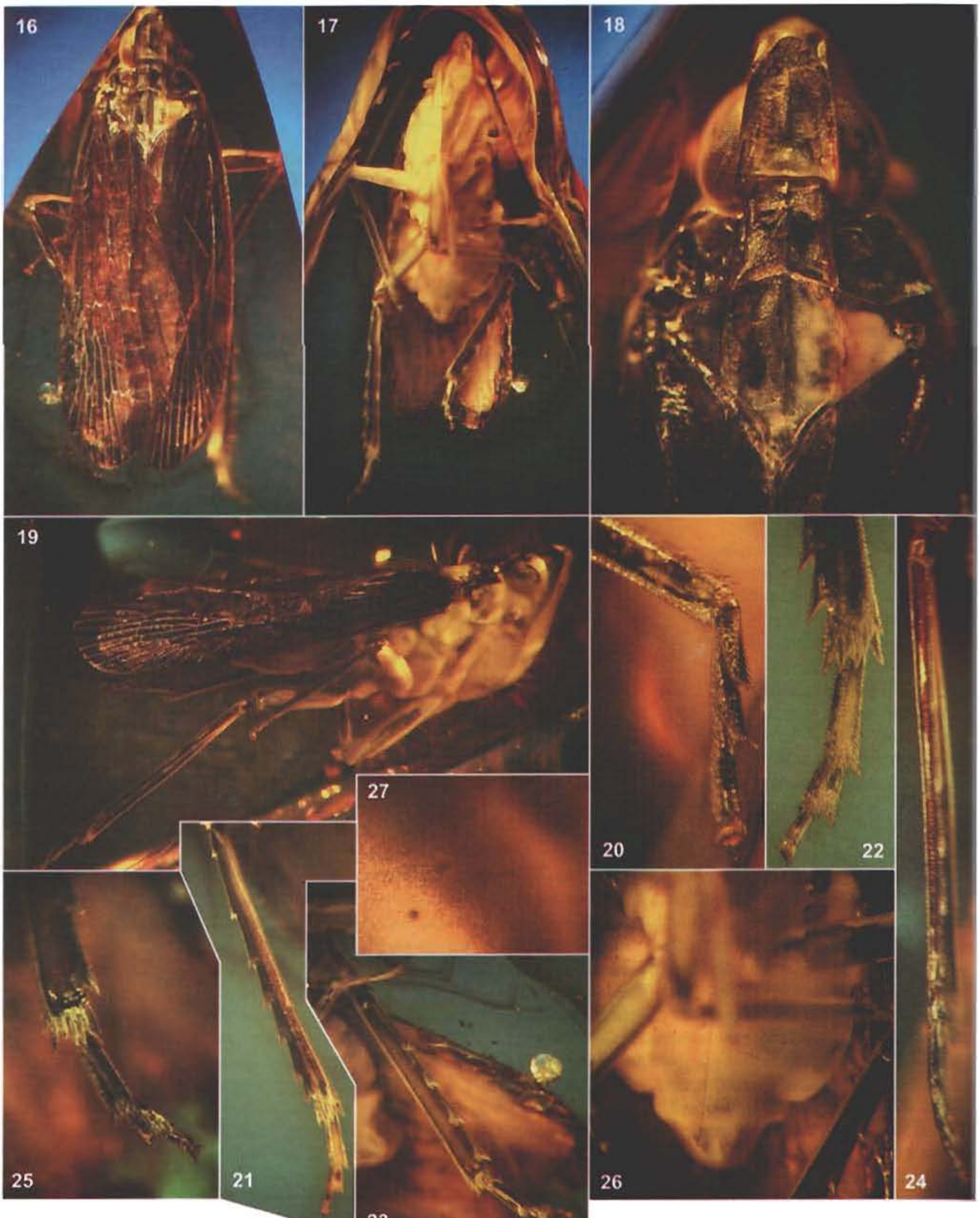


Figure 15. *Waghilde baltica* gen. and sp. nov. Abdomen. Scale bar: 1 mm.



Figures 16–27. *Waghilde baltica* gen. and sp. nov. (16) Specimen in amber, dorsal view; (17) specimen in amber, ventral view; (18) anterior part of the body; (19) specimen in amber, right lateral view; (20) right fore tarsus; (21) left hind leg; (22) left hind tarsus; (23) right hind leg; (24) right hind leg in lateral view; (25) right hind tarsus; (26) abdomen; (27) abdominal trichobothria.

are the only tribes of Achilinae with more than three lateral spines of the hind tibia. In Rhotalini the hind tibia is subquadrangular in cross section, while in Waghildini it is distinctly flattened. The structure of lateral spines differs in representatives of both tribes. In both tribes they have the structure of fused large socle and thick, short seta as postulated also for other Fulgoroidea (Emeljanov 1987, 2001, 2002). In Rhotalini the lateral spines are round, while in Waghildini both elements, socle and seta are flattened (Figs 13 and 14). Apical teeth in Waghildini are also different than in Rhotalini. In the latter there are 5–6 apical teeth arranged in a regular row of 1+4 or 1+5 teeth, while in Waghildini the number of apical teeth is 8–9, and the teeth are not arranged in regular row. Two small teeth in the second row of right hind tibia are of particular interest. Apical teeth of the basitarsomere and mid tarsomere, with exception of apical ones, are provided with subapical thick setae in Waghildini. Such an arrangement of subapical setae is known in Achilinae: Myconini, Achilini: Cixidiina and Tropiphlepsiini. In some other Achilinae, including Rhotalini, subapical setae are present only on the mid hind tarsomere (Emeljanov 1991, 1992). Regarding fossil representatives of Achilidae, subapical setae are present in *Niryasaburnia burmitina* (Cockerell, 1917) from the Lower Cretaceous Burmese amber (Szwedo 2004a), absent in *Acixiites* Hamilton, 1990, from the Lower Cretaceous of Brazil (Hamilton 1990) and in genera of Ptychoptilini from Eocene Baltic amber (Emeljanov 1990, Szwedo and Stroiński 2001). Emeljanov (1982) believed that the hind leg basitarsomere and mid tarsomere without subapical setae has to be regarded as a plesiomorphic condition within Fulgoroidea. Van Stalle (1986) postulated that chaetotaxy of the hind tarsomeres with a double row of a variable number of teeth and setae a plesiomorphic condition. Later, Emeljanov (1987) stated that the hind basitarsomere and mid tarsomere provided with subapical setae, is a feature believed to be a plesiomorphic condition within Fulgoroidea. This statement is also supported by the presence of subapical setae in extinct family Lalacidae from the Lower Cretaceous (Aptian) of Brazil (Hamilton 1990), and not formally described fossil Fulgoroidea from the Lower Cretaceous Lebanese and Jordanian ambers. Such a condition is to be found among families regarded as basal in phylogentic schemes: Cixiidae – some Pentastirini, and Dictyopharidae, Fulgoridae – Aluntini and Aphaenini (Emeljanov 1971, 1979, 1982). The function of the macrochaetae present in tarsomeres of many Fulgoroidea (Fulgoromorpha), and Cicadomorpha as well, is not thoroughly investigated (Dlabola 1988). Representatives of Fulgoroidea communicate by substrate-borne vibrations (Howarth et al. 1990; Tishechkin 1997, 1998, 2003). It has been postulated that subapical setae act as an organ of the sense of hearing during communication through the substrate of vibrations by drumming (Dlabola 1988). It is also probable that apical setae of fore and mid leg tarsomeres, very distinct in *Waghilde*, are involved in this process. To prove this hypothesis, further research is necessary. Trichobothria are present on abdominal sterna in the Fulgoroidea and various trichobothrial patterns are to be observed (Sweet 1996). These structures are of systematic usefulness (Szwedo 2004b), but are insufficiently elaborated. There are no exhaustive report on this structures among Achilidae (and other Fulgoroidea) as well, but trichobothria are to be observed in various tribes of Achilidae. Because of not perfect preservation of trichobothria in *Waghilde*, little can be said at this moment.

The relationship scheme of Achilinae proposed by Emeljanov (1992) did not include fossils. Waghildini could be placed close to Rhotalini and Mycarini, on the basis of retaining numerous lateral spines on hind tibia (plesiomorphic condition shared with Rhotalini) and not polymerized posterior branch of CuA on tegmen (apomorphic condition shared with other Achilinae). However, according to Emeljanov's scheme Rhotalini and Myconini form separate cluster, and Mycarini are opposed to the rest of Achilinae on the second branch of cladogram proposed by Emeljanov (1992). Tegmen and wing venation could relate Waghildini with Mycarini and Achilini: Cixidiina. The presence of subapical setae on both tarsomeres of hind leg (plesiomorphic condition?) is a feature shared by Waghildini and Myconini, Achilini: Cixidiina and Tropiphlepsini. It seems, that the exact placement of Waghildini in the phylogenetic scheme of Achilidae could not be solved at this moment.

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