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An extraordinary tribe of Tropiduchidae from the Eocene Baltic amber (Hemiptera: Fulgoromorpha: Fulgoroidea)

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Abstract

The new tribe Patollini **trib. n.** of the Tropiduchidae with the extinct genus *Patollo* **gen. n.**, comprising two species *Patollo natangorum* **sp. n.** and *P. aestiorum* **sp. n.** from Eocene Baltic amber is described. Taxonomic placement of some fossil taxa ascribed to Tropiduchidae is discussed. The classification of Tropiduchidae is discussed, as well as phylogenetic position and fossil record of Tropiduchidae and related taxa.

Key words: Patollini trib. n., *Patollo* gen. n., *Patollo* natangorum sp. n., *Patollo* aestiorum sp. n., Baltic amber, Palaeogene, classification, phylogeny, taxonomy, fossil record, Baltic amber, new tribe, new genus, new species.

Introduction

Fossil representatives of the family Tropiduchidae were described from both imprints and fossil resins. The oldest descriptions of taxa ascribed to this family comes from Germar & Berendt (1856) monograph of inclusions from the Eocene Baltic amber (Emeljanov 1983; Shcherbakov 2006). Other taxa from the Baltic amber were added by Szwedo (2000) and Szwedo & Stroiński (2010), and from imprints from the Eocene deposits of the Green River (Shcherbakov 2006).

The family Tropiduchidae Stål, 1854, is one of the smaller planthopper families comprising 575 described species in 164 genera (Yang et al. 1989; Shcherbakov 2006; Gnezdilov 2007; Bourgoin 2012). Tropiduchidae are distributed in the warmer regions of the world, feed on shrubs and trees, and some are crop pests. (Fennah 1982; Wilson et al. 1994; O'Brien 2002). The most recent higher classification of the family was provided by Fennah (1982) who recognized 15 tribes (three of them divided into subtribes), based on body structure and tegminal venation. This subdivision was primarily based on diagnostic characters without discussion of homology and evolutionary trends (Asche & Wilson 1989). The tribes and subtribes recognized by Fennah (1982) are as follows: Trypetimorphini Melichar, 1914, Neomatissini Fennah, 1982, Tambiniini Kirkaldy, 1907, Turneriolini Fennah, 1982, Paricanini Melichar, 1914, Isporisini Fennah, 1982, Eporini Fennah, 1982 (subtribes Eporina Fennah, 1982, Clardeina Fennah, 1982), Catullini Melichar, 1914, Cyphoceratopini Fennah, 1945, Tangiini Melichar, 1914 (subtribes Tangiina Fennah, 1982, Neotangiina Fennah, 1982), Alcestini Melichar, 1914, Remosini Fennah, 1982, Tropiduchini Melichar, 1914, Eutropistini Kirkaldy, 1906 (subtribes Duriina Fennah, 1982, Kazerunina Dlabola, 1977, Eutropistina Fennah, 1982) and Cixiopsini Fennah, 1982. Later, the extinct tribe Jantaritambiini Szwedo, 2000, described from Baltic amber was added (Szwedo 2000). Shcherbakov (2006) added another extinct tribe Emilianini, based on the imprint of tegmen from the Eocene of the Green River, Colorado. Subsequently, Szwedo & Stroiński (2010) added another extinct tribe from the Eocene Baltic amber - Austrini Szwedo et Stroiński, 2010. Gnezdilov (2007) transferred the Gaetuliina Fennah, 1978 from Nogodinidae to Tropiduchidae giving it tribal status, and Trienopini Fennah, 1954 from Issidae.

Material and methods

Specimens were examined under normal and polarized light, using an OLYMPUS SZH10 stereoscopic microscope. Drawings were made using an attached cameral lucida. Photographs were taken with use of OLYMPUS C-5060W digital camera attached to the stereoscopic microscope, and then readjusted using Combine ZP and Adobe Photoshop Elements 5.0 software.

Vein nomenclature follows the interpretation proposed by Szwedo & Żyła (2009) and Nel et al. (2012).

Systematics

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1946

Superfamily Fulgoroidea Latreille, 1807

Family Tropiduchidae Stål, 1854

Tribe Patollini trib. n.

Type genus: Patollo gen. n., here designated.

Diagnosis. The new tribe differs from other Tropiduchidae by the combination of characters as follows. Head with vertex wider than long in midline. Brachypterous, with costal area present, not reaching apex of clavus; nodal line absent, common portion of M and CuA present. Hind tibiae with three lateral spines. Male genital styles fused at base.

Description. Head with compound eyes wider than pronotum. Vertex distinctly wider than long in midline; with margins strongly carinate; vertex anteriorly widely angulate. Frons and clypeus smooth, lacking pustules or setae. Frons with median carina, lateral margins of frons carinate. Antennal pedicel longer than wide; plate organs, microsetae and macrosetae present only in distal half. Postclypeus without carinae. Apical segment of rostrum distinctly longer than broad. Pronotum short, with two distinct anterolateral carinae fused medially. Mesonotum widely rhomboid, lateral angles at about half of mesonotum length, close to the posterior margin of pronotum; mesonotum tricarinate, lateral carinae not connected anteriorly; scutellum separated from mesonotum by transverse groove.

Tegmen ovoid, with full venation developed, brachypterous; anterior margin strongly convex, anteroapical angle widely angulate, apex rounded, posteroapical angle widely rounded, clavus with apex reaching to about ²/₃ of tegmen length. Costal area about as wide as costal cell, subequal throughout, with apex not exceeding apex of clavus, with transverse veinlets. Costal cell with transverse veinlets. Basal cell elongate, stems Sc+R and M leaving basal cell with a common stalk, separately from CuA stem. Forking pattern of stems Sc+R, M and CuA not regular, variable on left and right tegmina, but with common portion of branches M and CuA present. Nodal line absent, transverse veinlets not forming regular pattern or cells. Clavus with transverse veinlets.

Hind tibiae with three lateral spines in distal half and apical row of teeth. Basitarsomere longer than second tarsomere, with apical row of teeth and subapical setae. Second tarsomere with median portion arcuate, covered with setae. Basitarsomere about as long as combined length of second and third tarsomeres.

Abdominal segments III-VIII subequal in length. Pygofer narrow, about 3 times as high as long in the middle at ventral margin. Genital styles lobate, wide, with subapical processes, near the margin of pygofer, fused at base. Anal tube not exceeding length of genital styles, with anus in the middle.

Composition. Patollo gen. n.

Genus Patollo Szwedo et Stroiński gen. n.

Type species: Patollo natangorum Szwedo et Stroiński sp. n., here designated.

Composition. Two species. Patollo natangorum sp. n., P. aestiorum sp. n.

Age and occurrence. Eocene, Baltic amber.

Etymology. The generic name is derived from the name of the Old Prussian (Baltic Prussian) god of war, the underworld, and the dead – Patollo. Gender: masculine.

Diagnosis. Head with vertex wider than long in mid line. Metatibio-tarsal formula 8: 2+(7): 2(0); Anal tube narrow, about 5 times as long as wide. Male genital style in lateral aspect, about as long as high, with small spine on dorsal margin at level of pygofer apex.

Description. Vertex with margins strongly carinate, anterior aspect of vertex broadly angulate, lateral margins subparallel, elevated, posterior margin broadly concave. Disc of vertex concave, smooth, with incomplete carinae (median or lateral ones). Frons and clypeus smooth, lacking pustules or setae; frons with median carina reaching frontoclypeal suture, lateral margins of frons carinate. Compound eye bulging, about as broad as long, posteroventrally delimited by narrow callus. Antennal fovea placed below the compound eye, elevated at posterior margin; pedicel club-like, longer than wide, arista long, placed centrally on pedicel. Postclypeus without carinae. Rostrum with apex slightly exceeding mesocoxae, apical segment of rostrum distinctly longer than wide.

Mesonotum in apical portion delicately wrinkled. Stem of M forked apicad of fork of stem of Sc+R.

Pro- and mesofemora not flattened, subequal in length; pro- and mesotibiae subtrapezoid in cross section, subequal in length. Profemora and protibiae and mesofemora and mesotibiae subequal in length, respectively. Metafemora slightly flattened, distinctly shorter than metatibiae. Metacoxae very well developed, enlarged, with meracantha distinct, subtriangular with acute apex. Metatibiae dilated apically, flattened to concave in apical portion.

Male. Pygofer in lateral view wider in apical portion with posterodorsal angle widely rounded, without processes. Anal tube narrow, without processes, apical portion, apicad of anus, in lateral view narrower than basal one. Genital styles with rounded apex, lower margin with small tooth-like expansion near base.

Female unknown.

Patollo natangorum Szwedo et Stroiński, sp. n.

(Figs 1–17)

Diagnosis. Disc of vertex without median carina; two incomplete and weak lateral carinae from anterior margin of disc of vertex directed posteriorly, these are not reaching half of vertex length measured in the middle.

Description. Total length 4.9 mm, head with compound eyes about 2.16 mm wide, length of vertex in mid line 0.34 mm, 0.4 mm at lateral margin, width of vertex 1.1 mm; length of frons in mid line 1.28 mm, 1.2 mm at lateral margin; apical segment of rostrum 0.33 mm long; antennal scape 0.11 mm long, pedicel 0.23 mm long, arista 0.86 mm long.

Length of pronotum 0.32 mm, width of disc of pronotum 1.52 mm, length of mesonotum+scutellum 0.84 mm, width of mesonotum at base 1.28 mm.

Pronotum slightly shifted from mesonotum, hence the arcuate anterior of mesonotal ridge is visible. Anterior mesonotal ridge strongly arcuate, reaching posterior margin of mesonotum.

Length of tegmen about 2.37 mm, width of tegmen about 1.06 mm; length of clavus 1.52 mm.

Profemur about 1 mm long, protibia 1.04 mm, protarsus with claws 0.43 mm, first tarsomere 0.16 mm, mid tarsomere 0.16 mm, apical tarsomere 0.21 mm, tarsal claws 0.07 mm. Mesotibia 1.18 mm, mesotarsus with tarsal claws 0.33 mm, basitarsomere 0.17 mm, mid tarsomere 0.17 mm, apical tarsomere with tarsal claws 0.33 mm. Metafemur 1.15 mm long, metatibia 1.82 mm long, 0.26 wide at apex, metatarsus with tarsal claws 0.66 mm long, basitarsomere 0.37 mm long, about 0.15 mm wide at apex, midtarsomere 0.21 mm long, 0.13 mm wide at apex, apical tarsomere 0.21 mm long.

Abdomen with genital segment 2.5 mm long. Anal tube 1.07 mm long, 0.2 mm wide. Pygofer 1.61 mm high, 0.63 mm long at upper margin 0.43 mm long in the narrowest point, 0.5 mm near ventral margin. Genital style 0.91 mm long, 1 mm wide.

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FIGURES 1–8. *Patollo natangorum* **gen. et sp. n.** 1. anterior portion of body; 2. head in left lateral view; 3. left tegmen venation; 4. right tegmen venation; 5. left hind leg; 6. apex of hind tibia; 7. anal tube in dorsal view; 8. apex of male abdomen, left lateral view.

Left tegmen. Stem Sc+R forked in basal half of tegmen, basad of stem M forking; apicad of claval veins Pcu and A_1 junction. Branch ScRA₁ forked basad of stem M forking, RA forked basad of fork of RP; stem RP forked slightly basad of fork of branch M_{1+2} . Stem M forked at about half of tegmen length; branch M_{3+4} fused with branch CuA₁, which extends to the margin. Stem CuA forked slightly apicad of stem M forking, slightly basad of costal area apex. Claval veins Pcu and A_1 connected slightly basad of half of clavus length.

Right tegmen. Stem Sc+R forked slightly apicad of stem CuA forking, well basad of stem M forking. Branch RA probably with three terminals, stem RP forked apically at level of claval apex. Stem M forked basad of claval apex; branch M_{1+2} forked apically, branch M_{3+4} fused with CuA₁ for a long distance, then terminal M_3 separated near

apex. Stem CuA forked well basad, at basal $\frac{1}{3}$ of tegmen length, basad of claval veins junction. Claval veins Pcu and A₁ connected at half of tegmen length. The details are difficult to discern because of a milky veil obstructing the specimen.

Etymology. The specific epithet is derived from the Natangi—the Old Prussian tribe inhabiting the area between the rivers Pregel (now Pregolya) and Alle (now Łyna) during the Middle Ages.



FIGURES 9–13. *Patollo natangorum* **gen. et sp. n.** 9. specimen in amber, left lateral view; 10. anterior portion of body; 11. anterior portion of body, left laterodorsal view; 12. head in left lateral view; 13. hind legs.

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FIGURES 14–17. Patollo natangorum gen. et sp. n. 14. left tegmen; 15. mid and hind legs; 16. left hind tarsus; 17. apex of male abdomen.

Age and occurrence: Baltic amber, Middle Eocene. This fossil resin is aged within the range of 38–47 Ma (Ritzkowski 1997; Perkovsky *et al.* 2007). Absolute dating analyses of glauconites from Sambia Peninsula showed that the "blue earth" formation (amber bearing Prussian Formation) is allocated to the Middle Eocene (Lutetian: 44.1 ± 1.1 Ma) and is thus significantly older than previously assumed (Wappler 2003, 2005). Limnic sediments of Eckfeld Maar, aged 44.3 ± 0.4 Ma, correlate with K-Ar radiometric data from the Sambia Peninsula and contain

insect genera known only from Baltic amber (Wappler 2005). However, assumptions on the Middle Eocene age of Baltic amber was discussed by Perkovsky *et al.* (2007), and the Upper Eocene (Bartonian/Priabonian: 37.7 ± 3 Ma) age of the Prussian Formation is preferred by these authors. Weitschat & Wichard (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.

Material examined. Holotype, male. Specimen No. MIBUG 5419 (AUF 084JS), Coll. Jacek Serafin, Piaseczno, deposited in the Museum of Amber Inclusions, University of Gdańsk, Poland. Right side of the inclusion covered with a milky veil. Syninclusions: fragment of unidentified plant, a few bubbles of gas.

Patollo aestiorum Szwedo et Stroiński, sp. n.

(Figs 18-30)

Diagnosis. Disc of vertex with incomplete and weak median carina posteriorly, not reaching half of vertex length.

Description. Total length 5.33 mm, head with compound eyes 1.57 mm wide, length of vertex in mid line 0.28 mm, 0.35 mm at lateral margin, width of vertex 0.86 mm; length of frons in mid line 1 mm, 1.14 mm at lateral margin, length of postclypeus in mid line 0.67 mm, length of anteclypeus in mid line 0.5 mm, length of clypellus 0.14 mm, length of rostrum 0.93 mm, subapical segment 0.41 mm, apical segment 0.4 mm; length of second antennal joint 0.29 mm, length of antenna 0.78 mm.

Length of pronotum 0.28 mm, width of disc of pronotum 0.86 mm between anterolateral carinae at posterior margin, about 1.37 mm, length of mesonotum+scutellum 0.71 mm, width of mesonotum at base 1.2 mm.

Length of tegmen 2.05 mm, width of tegmen 1.05 mm; length of clavus 1.5 mm.

Profemur 1 mm long, fore tibia 0.86 mm, protarsus with claws 0.43 mm, first tarsomere 0.17 mm, mid tarsomere 0.17 mm, apical tarsomere 0.24 mm, tarsal claws 0.07 mm. Mesofemur 1 mm, mid tibia 1.14 mm, mesotarsus with tarsal claws 0.5 mm, basitarsomere 0.2 mm, mid tarsomere 0.2 mm, apical tarsomere 0.29 mm. Metacoxa 0.22 mm long, metatrochanter 0.22 mm long, metafemur 1 mm long, metatibia 1.8 mm long, 0.25 wide at apex, metatarsus with tarsal claws 0.64 mm long, basitarsomere 0.36 mm long, 0.16 mm wide at apex, midtarsomere 0.23 mm long, 0.13 mm wide at apex, apical tarsomere 0.23 mm long.

Abdomen with genital segment 3.33 mm long. Anal tube 1.07 mm long, 0.2 mm wide. Pygofer 1.43 mm high, 0.64 mm long at upper margin 0.4 mm long in the narrowest point, 0.47 mm near ventral margin, 0.36 mm in mid line at ventral margin. Genital style 1.07 mm long, 1.14 mm wide.

Tegmen length : width ratio 1 : 1.95, claval apex reaching 0.73 of tegmen length. Clavus with veinlet between stem CuA and CuP, apicad of claval veins junction, free portion of vein Pcu measured from anterior claval angle to claval veins junction 1.8 times longer than common claval vein Pcu+A₁. Metatibio-tarsal formula 8 : 2+(7) : 2 (0); basitarsomere longer dorsally than wide between tips of outermost teeth (2.45 : 1); mid tarsomere longer dorsally than wide between tips of outermost teeth (2.45 : 1); mid tarsomere longer dorsally than wide between tips of outermost teeth (1.6 : 1). Anal tube narrow, about 5 times as long as wide, with lateral margins subparallel, apical margin straight. Male genital style in lateral aspect, about as long as high, with small appendix on dorsal margin at level of pygofer apex, with indistinct lateral keel; apical margins thickened; covered with short, thick setae.

Terminal system of branches RA, RP and M forking disorganized, vary on left and right tegmen; veinlets on corium and membrane between longitudinal branches not regular, vary on left and right tegmen. Variability in tegminal venation and veinlets system of left and right tegmina as in figures.

Left tegmen. Stem Sc+R forked slightly anteriad of stem M forking and anteriad of stem CuA forking, branch ScRA₁ forked at level of stem M forking; branch RA forked twice reaching margin with three terminals; branch RP forked slightly basad of level of claval apex. Stem M forked at level of claval veins junction, branch M_{1+2} forked at level of contact of fused claval veins with claval margin, branch M_1 reaching apex with two terminals, branch M_2 reaching margin with two terminals; branch M_{3+4} fused for a long distance with branch CuA₁, basad of claval apex, then common branch forked slightly before apex. Stem CuA forked slightly apicad of claval veins junction, branch CuA₁ fused with M_{3+4} then with M_4 , branch CuA₂ not forked before apex. Claval vein Pcu and A₁ fused apicad of half of length of clavus.

Right tegmen. Stem Sc+R forked slightly apicad of claval veins junction, branch ScRA₁ forked at level of stem M forking; ScRA₁ forked before reaching the margin; branch RA forked before reaching the margin; branch RP

forked twice before the margin, reaching it with three terminals. Stem M forked slightly apicad of claval veins junction, branch M_{1+2} reaching the margin with as single terminal (but see discussion); branch M_{3+4} forked at level of apex of costal area, branch M_3 forked just after the apex of clavus; branch M_4 fused with CuA₁ for a distance, reaching margin together with CuA₁. Stem CuA forked just before margin, slightly apical of claval apex. Claval veins Pcu and A₁ fused at about half of length of clavus.

Remarks. The venation of the right wing of *P. aestiorum* can be interpreted as described above or, alternatively, the stem M_{1+2} is forked distinctly basad of the claval apex, with blind branch M_2 . Another equally probable interpretation is that branch M_2 is "broken" and the distal portion of the branch M_2 is fused with M_3 for a distance with branch M_3 re-emerging at the level of claval apex.

Age and occurrence. Eocene, Baltic amber, for details see comments in the section on P. natangorum.

Etymology. The specific epithet is derived from the name of the people inhabiting the eastern Baltic Coast during the Antiquity – Aestii.



FIGURES 18–23. *Patollo aestiorum* **gen. et sp. n.** 18. anterior portion of body; 19. venation of left tegmen; 20. venation of right tegmen; 21. right hind leg; 22. right hind tarsus; 23. apex of male abdomen.

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FIGURES 24–30. *Patollo aestiorum* **gen. et sp. n.** 24. specimen in amber, right lateral view; 25. specimen in amber, left lateral view; 26. anterior portion of body, dorsal view; 27. anterior portion of body, right laterodorsal view; 28. hind legs; 29. hind tarsi; 30. apex of male abdomen.

Material examined. Holotype, male, Nr. 373 B; collection of Mr. Carsten Gröhn, Glinde, Germany, to be deposited in the Geologisch-Paläontologisches Institut, Hamburg Universität, Germany. Left side covered with milky veil, abdominal segment exposed, very probably due to the activity of decaying gases. Syninclusions: a bunch of stellate hairs, very tiny apterous aphid.

Discussion

The tribe Patollini from Eocene Baltic amber clearly differs from any other tribe of the Tropiduchidae. Brachyptery combined with the presence of a short costal area are the most striking features of the group. A short costal area with transverse veinlets, with the apical portion not reaching the apex of the clavus is present in the fully winged, recent tribe Alcestini. Also, the ovoid shape of the wing resembles that of Alcestini, as well as lack of a nodal line (however, venation in the Alcestini is more regular and well developed). The short tegmina, lack of a nodal line and presence of veinlets in the costal cell somewhat resembles the Austrini, and the head characters of the two tribes are similar, i.e. vertex wider than long in midline. The costal area with veinlets and the head with vertex wider than long are also present in the Gaetuliini (both extant species and fossils from Eocene Baltic amber). Meracantha [(post-coxal process of Fennah (1982)] of the Patollini is stout and spine-like, as in the Austrini, however, the metacoxa is enlarged and together with metepimeron covers a large area. Fennah (1982: 632) stated that the form of the process is useful for separating genera, but of limited value for distinguishing tribes. The metatibia with three lateral spines is present in the extant tribes Alcestini, Cyphoceratopini, Remosini and Tangiini, as well as in extant and fossil Gaetuliini. The bilaterally symmetrical genital styles fused at base are present in most extant tribes of Tropiduchidae.

The diversity of Tropiduchidae known from Eocene Baltic amber is quite high. There are three extinct tribes known, Jantaritambiini, Austrini and Patollini, and representatives of Gaetuliini, which include extant species, were reported as well (Szwedo & Stroiński 1999, 2010; Szwedo 2000). This suggests rapid diversification of the Tropiduchidae during the Palaeogene.

Most planthoppers are macropterous, but brachyptery is common in several families (O'Brien & Wilson 1985). Brachyptery was defined by Metcalf (1950) as tegmina with reduced venation, covering only the basal segments of the abdomen. Capinera (2008) defined brachyptery as having short wings that do not cover the abdomen or nearly so. Asche (1985) discussed pterygopolymorphic species of Delphacidae that had various types of tegmina and hind wings. O'Brien & Wilson (1985) stated that brachyptery in planthoppers may range from a partial to an almost complete reduction in the size of the hind wings with a relatively long tegmina, to the apparent absence of hind wings and great shortening of the tegmina. The problem of wing reduction in the Hemiptera was discussed by Kerzhner (1981) based on his observations of Nabidae. He defined macropterous forms as those having normally developed tegmina and hind wings with complete venation, more or less exceeding the apex of the abdomen. Submacropterous forms are those with hind wings distinctly shorter than tegmina and tegmina often slightly shorter and narrower than those of macropters. Subbrachypterous forms are those with the tegmina merely reaching the apex of the abdomen and with strongly reduced hind wings. Brachypterous (micropterous) forms are these with the tegmina reaching $\frac{1}{3}$ of the body length, reduced membrane of the tegmen, and eubrachypterous (micropterous) are those with the tegmina shorter, membrane reduced to narrow appendix or missing, clavus and corium fused and hind wings in the form of short and small scales or completely absent. Metcalf (1950) defined macropterous tegmina as usually longer than the abdomen, frequently much longer, with fully developed venation, and koeliopterous tegmina as those of moderate length, covering most of the abdomen and with fairly developed venation. The latter term (used as coeliopterous) was subsequently used by Fennah (1982) to describe tegmina of some tropiduchid tribes. The tegmina of Patollini trib. n. match the definitions of brachyptery, in terms of their length, however, they have fully developed venation and the membrane is not shortened or reduced.

Further study of the external morphological structures, venation patterns of extant and extinct taxa, external and internal genital characters of both males and females is necessary in order to understand the evolutionary relationships of this family and its relatives.

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