



The last batrachideine of Europe: A new genus and species of pygmy grasshopper (Orthoptera: Tetrigidae) from Eocene Baltic amber

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Abstract

A new genus and species of pygmy grasshopper (Orthoptera: Tetrigidae) is described from Eocene Baltic amber. *Danatettix hoffeinsorum* **gen. et sp. nov.** is assigned to the subfamily Batrachideinae based on antennae with more than 19 antennomeres, sulcate mesofemora, and rectangular paranota. This species is readily distinguished from other batrachideines by a markedly produced vertex, pronotum with divergent internal and external lateral carinae, and highly setiferous female lateral basivalvular sclerite with scabrose integument. The morphology of *Danatettix* suggests placement within the here defined *Tettigidea* genus group (comprising *Eutettigidea* Hancock, 1914, *Paurotarsus* Hancock, 1900, and *Tettigidea* Scudder, 1862) and suggests that the latter had diverged from the new *Scaria* genus group (comprising *Eotetrix* Gorochov, 2012, *Rehndium* Grant, 1956 and *Scaria* Bolívar, 1887) by the Early Eocene.

Key words: Caelifera, Tetrigoidea, pygmy locusts, grouse locusts, groundhoppers, Cenozoic, Paleogene, Baltic amber, fossil insects

Introduction

The Tetrigidae (grouse locusts, groundhoppers, pygmy locusts) are an ancient and speciose family, and within Caelifera, are second only to the Acrididae in terms of diversity (Heads, 2009; Song *et al.*, 2015). Currently more than 2,000 species have been described in over 270 genera (Cigliano *et al.*, 2019), but of this number, only twelve (including the new taxon described herein) are known from fossils (Heads *et al.*, 2014). Six of the twelve known fossil Tetrigidae occur in fossil resins and the remainder are compression fossils (Table 1). Well-known for their cryptic morphology, tetrigids are readily identified by their extended pronotum, which typically covers at least the length of the abdomen and often beyond. Members of the subfamily Batrachideinae (long-horned pygmy grasshoppers) are distinguished from members of all other tetrigid subfamilies by five distinctive apomorphies: (1) antennae with more than 19 antennomeres; (2) rectangular paranota; (3) sulcate dorsal margin of the mid-femora; (4) tegmina with yellow markings; and (5) female spermatheca with two diverticula (Grant, 1962). Estimated time of divergence of Batrachideinae and other tetrigid subfamilies is more than 135 Ma (Song *et al.*, 2015).

Material and methods

The specimens studied here reside in the collection of Christel and Hans Werner Hoffeins (CCHH) of Hamburg, Germany, and will ultimately be deposited in the Senckenberg Deutsches Entomologisches Institut in Müncheberg, Germany. Specimen 1084-3 was prepared according to Hoffeins (2001) and is untreated via autoclave. One small triangular section was removed using a jeweler's saw in order to provide a clearer view of the anterior aspect. This now exposed section was sealed using EpoTek 301-2 resin painted on the surface of the amber. Specimen 1084-4

is an embedded piece of amber that was prepared as per Hoffeins (2001) and is untreated via autoclave. Specimen 1084-5 is a large and unembedded piece of Baltic amber that was treated in an autoclave as per Hoffeins (2012) and polished as per Hoffeins (2001). Images were taken using a Zeiss SteREO Discovery V.20 stereomicroscope with a Plan-Apochromat S 0.63x objective and an AxioCam HRc Rev. 3 digital camera. Measurements were taken with the Zen 2 (Blue edition) software. Stacked images were processed with Helicon Focus 6 and were stitched into a final panorama using Adobe Photoshop CC. Illustrations were created using Adobe Illustrator CC by the first author. Morphological terminology, measurements and description of important diagnostic characters follows Grant (1956a, 1956b, 1962, 1966), Heads (2009), and Heads *et al.* (2014).

TABLE 1. List of fossil Tetrigidae (modified from Heads *et al.*, 2014). Asterisks indicate that the whereabouts of the type specimen is unknown.

Taxa	Locality	Geological Period
<i>Acrydium bachofeni</i> Zeuner, 1937	Baltic amber	Middle Eocene
<i>Antillotettix electrum</i> Heads, 2009	Dominican amber	Early Miocene
<i>Archaeotettix locustopseiformis</i> Sharov, 1968	Turga Fm, Transbaikalia, Russia	Early Cretaceous
<i>Baeotettix lottiae</i> Heads, 2009	Dominican amber	Early Miocene
<i>Danatettix hoffeinsorum</i> , Thomas, Heads, Skejo, this paper	Baltic amber	Middle Eocene
<i>Electrotettix attenboroughi</i> Heads & Thomas, 2014	Dominican amber	Early Miocene
<i>Eoteterix unicornis</i> Gorochoy, 2012	Green River Fm, Wyoming, USA	Middle Eocene
<i>Prototettix reductus</i> Sharov, 1968	Turga Fm, Transbaikalia, Russia	Early Cretaceous
<i>Succinotettix chopardi</i> Piton, 1938*	Baltic amber	Middle Eocene
<i>Tettigidea gracilis</i> Heer, 1865*	Oeningen, Switzerland	Late Miocene
<i>Eozaentetrix wittecki</i> Zessin, 2017	North Jutland, Denmark	Early Eocene
<i>Eozaentetrix furi</i> Zessin, 2017	North Jutland, Denmark	Early Eocene

Systematic paleontology

Order: Orthoptera Olivier, 1789

Suborder: Caelifera Ander, 1936

Superfamily: Tetrigoidea Rambur, 1838

Family: Tetrigidae Rambur, 1838

Subfamily: Batrachideinae Bolívar, 1887

Tribe: Batrachideini Bolívar, 1887

***Danatettix* gen. nov.**

[urn:lsid:orthoptera.speciesfile.org:TaxonName:507395]

Type species. *Danatettix hoffeinsorum* sp. nov. by monotypy.

Diagnosis. The genus is differentiated from all other Batrachideinae by the following characters: (1) presence of divergent internal and external lateral carinae on the pronotum; (2) antennal flagellomeres of relatively equal length; (3) pronotum with subquadrate lobe and broadly curved but shallow humeral sinus; (4) tegminal sinus sharply angled; (5) pronotum with slight undulation along its length; (6) truncated anterior margin of the pronotum; and (7) posterior pronotal margin forming a sharp and slightly downturned acuminate process.

Etymology. The genus name honors Katie Dana, the first author's wife, without whom he would never have become interested in entomology. The suffix “*tettix*” is Greek and means “grasshopper.”

***Danatettix hoffeinsorum* sp. nov.**

[urn:lsid:orthoptera.speciesfile.org:TaxonName:507396]

Figs 1–10

Type material (3 specimens). (1/3) Holotype: CCHH 1084-4 of approximately 22 x 15 x 5mm, adult female Tetrigidae. Emulsion covering much of the dorsal surface of the specimen. One syninclusion present within the piece: one mite (Arachnida) of indeterminate identification. Paratypes: (2/3) CCHH 1084-3, well-preserved nymphal male in a piece of amber approximately 20 × 20 × 11 mm. Three syninclusions are also present within the piece: two springtails (Collembola: Entomobryomorpha); and a wasp (Hymenoptera: Bethyridae); (3/3) CCHH 1084-5, well-preserved nymphal male in a piece of amber approximately 50 × 27 × 10 mm. One syninclusion is also present within the piece: a fragmentary fly (Diptera: Dolichopodidae).

Age. Baltic amber is generally considered to be about 46 million years old.

Diagnosis. As for genus (see above), by monotypy.

Description of holotype (1084-4)

Head. Head hypognathous and dorsoventrally elongate. Integument finely granulose. Eyes globose. Median carinula slight, not extending above eye line, and not projecting anteriorly beyond eyes. Anterior margin of the fastigium truncated. Lateral fovea unpronounced. Frontal costal ridge long, bifurcates between the compound eyes, below fastigial ridge and just above the lateral ocelli and continues roughly parallel until its terminus on either side of the median ocellus. Clypeus and labrum mostly obscured by emulsion. Genae slightly inflated. Prominent lateral ridge on genae extending dorsoventrally from just below level of median ocellus to the frontoclypeal margin. Deep genal-furrow present anterior to the genal ridge. Mandibles obscured by optical discontinuity and emulsion. Right labial palpa not visible. Left maxillary palpa visible, robust, especially distal segment. Left and right labial palpa obscured by optical discontinuity and emulsion. Antennae with 20 segments including scape and pedicel. Scape and pedicel of both antennae mostly obscured by emulsion and optical discontinuity. Flagellomeres two and three are shorter than flagellomere one. All others relatively equal in length.

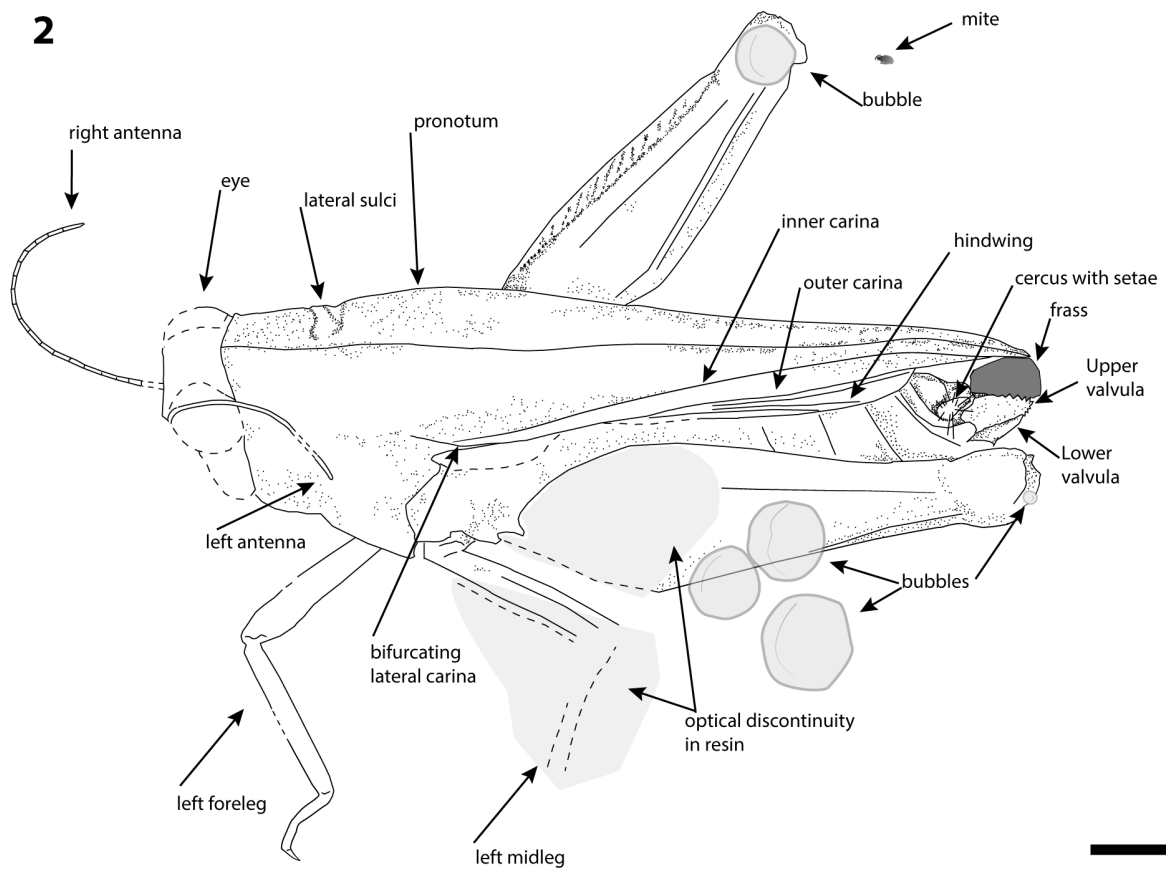
Thorax. Pronotum c. 9.8 mm in length. Pronotum relatively flat with slight undulation along its length (figure 1). Strongly defined median and lateral carinae. Lateral carina bifurcates at c. 3 mm from apical margin of pronotum (figure 2) into inner and outer lateral carinae. Anterior margin of pronotum possessing slight apically curved projection above the head. Posterior margin of pronotum ending with sharp and slightly downturned acuminate process. Pronotum with three transverse sulci, none cutting median carina, two cutting lateral carina before bifurcation point (figure 2). Humeral sinus broad, shallowly rounded. Tegminal sinus with relatively shallow invagination and sharp but apically rounded angle. Tegmen mostly obscured by cracking and emulsion. Wings present and terminate at the posterior-most tergite. Ventral surface of thorax sparsely populated with setae. Left prothoracic leg relatively robust, hexagonal in cross section with angles obtuse. Three pulvilli present on tarsi. Left mesothoracic leg thin, hexagonal in cross section with angles more acute and with more defined carinae than prothoracic leg. Obvious sulcus present along mesofemora. Tarsi missing from left mesothoracic leg. Emulsion over left metathoracic leg obscuring features of femur and tibia. Right prothoracic leg missing. Right mesothoracic leg missing. Right metathoracic tibia relatively straight with minor denticles sparsely distributed along ventral carinae. Tibio-tarsal junction of metathoracic legs possess four spurs. Four pulvilli present. Three on the proximal segment and one on the mid segment. Tarsal pulvilli obliquely angular. Tarsi three-segmented with two ungues and two ventral-facing unguis setae.

Abdomen. Abdomen c. 6 mm from posterior-most tip of subgenital plate to thoracic junction. Dorsal surface obscured by pronotum, wings, and emulsion. Left and right cerci visible, cone-shaped, with prominent setae on all surfaces. Subgenital plate steeply curved upward, acuminate tip, possessing denticles on dorsal surface and sparse setae across the ventral surface. Large piece of frass between abdominal and pronotal terminus.

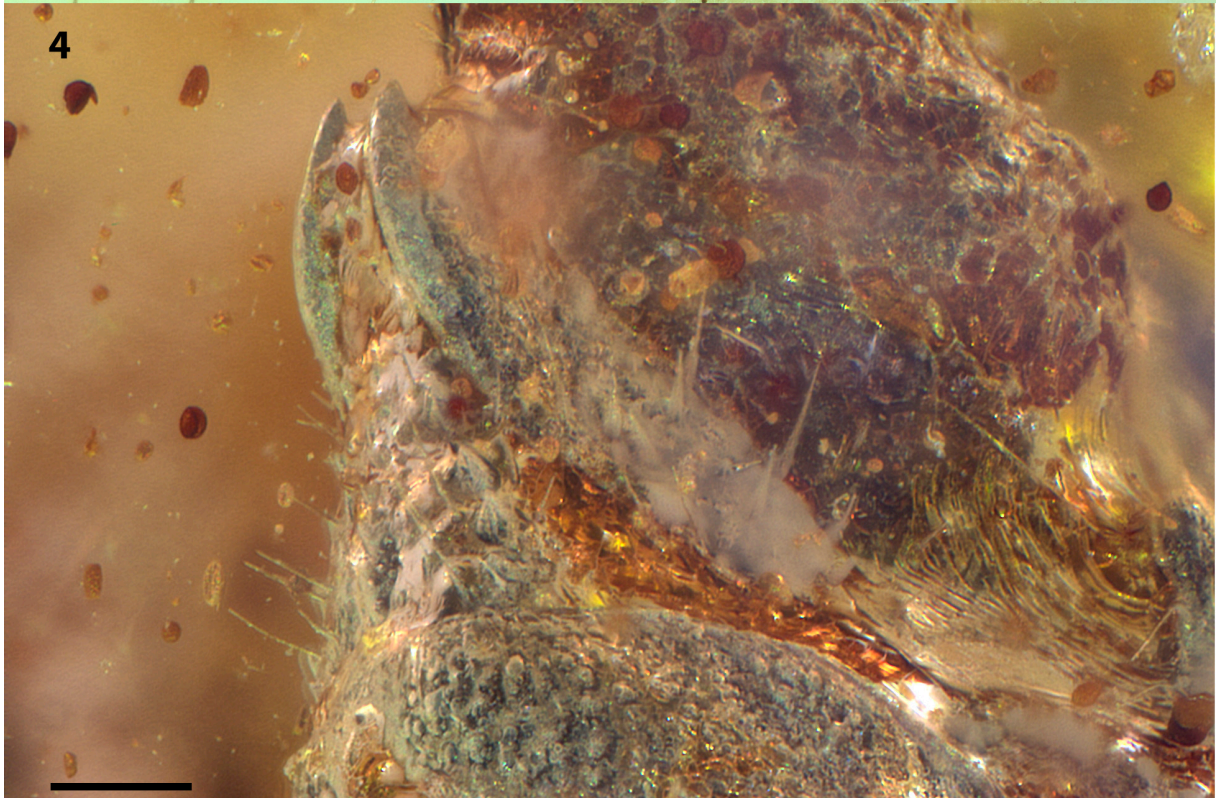
Etymology. The specific epithet honors Christel and Hans Hoffeins whose efforts in collecting Baltic amber have led to numerous important discoveries.

Description of paratype (1084-3)

Head: Head hypognathous and dorsoventrally elongate. Integument finely granulose. Eyes globose and acutely rounded ventrally. Subocular furrow slight. Vertex extending just slightly above eye line but barely projecting anteriorly beyond eyes. Fastigial horns present and rise to just below height of the median carinula (figure 5). Fastigial



FIGURES 1–2. FIG 1. Dorsal oblique view of holotype 1084-4 *Danatettix hoffeinsorum* (scale bar = 1 mm). FIG 2. Line drawing of holotype 1084-4 *Danatettix hoffeinsorum* (scale bar = 1 mm)



FIGURES 3–4. **FIG 3.** Ventral view of holotype 1084-4 *Danatettix hoffeinsorum* (scale bar = 1 mm). **FIG 4.** Close-up ventral view of ovipositor valvulae and subgenital plate of holotype 1084-4 *Danatettix hoffeinsorum* (scale bar = 0.2 mm)

ridge unpronounced; rounded. Lateral fovea deep and triangular in orientation. Median carinula somewhat prominent, slightly higher than vertex and extending to the posterior of the head capsule. Frontal costal ridge pronounced and projects anteriorly beyond eyes, sharply bifurcates c. 0.2 mm below fastigial ridge and begins to angle inward just below the antennal torulae eventually joining again c. 1 mm below the bifurcation; the median ocellus located just above this bifurcation. Lateral ocelli present c. 0.1 mm above antennal torulae. Clypeus mostly obscured by optical discontinuity (figure 6), but fronto-clypeal margin is visible though unremarkable. Labrum only partially visible in anterior view but has greater visibility from lateral oblique view. Mandible robust. Maxillary palpal segments visible and robust, especially apical segment. Left labial palp mostly obscured by emulsion, right obscured by optical discontinuity. Left antennae with at least twelve segments. Right antennae with twenty segments including scape and pedicel. Scape laterally compressed. Pedicel rounded, robust, larger diameter at posterior than anterior end by approximately half the apical diameter (c. 50 μ m).

Thorax: Pronotum c. 5 mm in length with slight anterior projection of c. 0.1 mm. Apex of pronotum slightly upturned and ending in a sharp point. Median carina posteriorly low but with a sweeping rise halfway to the anterior margin before plateauing at the height of the vertex. Lateral carinae forming low ridges along entire length from posterior apex until smoothing into the transverse sulci c. 0.8 mm from the left lateral anterior margin. Lateral carina bifurcates c. 1.75 mm from the left lateral anterior margin of the pronotum into inner and outer lateral carinae. Lateral carinae very slight along the length of the inner branch and slightly more pronounced along the outer branch. Humeral sinus broad and shallowly rounded. Tegminal sinus not very pronounced at this instar, with minor invagination that is somewhat rounded. Lateral lobes broad and gently rounded. Pronotum cut by two sulci that cross the lateral but not the median carina. Coarsely granulate integument with larger tubercular ornament on anterior margin of pronotum near transverse sulcus. Finely granulate integument at pronotal margin above tegmen.

Coxae robust on all legs. Trochanter thinner in pro- than meso- and metathoracic legs. Pro- and mesofemora mildly carinate on dorsoventral surfaces with obvious sulcus along mesofemora. Pro- and mesofemora quadrate in cross section. Fine denticular ornamentation along dorsoventral carinae of all legs. Pro- and mesothoracic tibiae quadrate in cross section. Metathoracic tibiae quadrate in cross section. Distal ventral margin of carinate processes on foretibiae with small spines. Tibio-tarsal junction of metathoracic legs possess four spurs. Pro- and mesothoracic tarsi with three pulvilli. Metathoracic tarsi with four pulvilli, three on basitarsus and one on the mid segment. Tarsi are three-segmented with two ungues and two ventral-facing unguisetae.

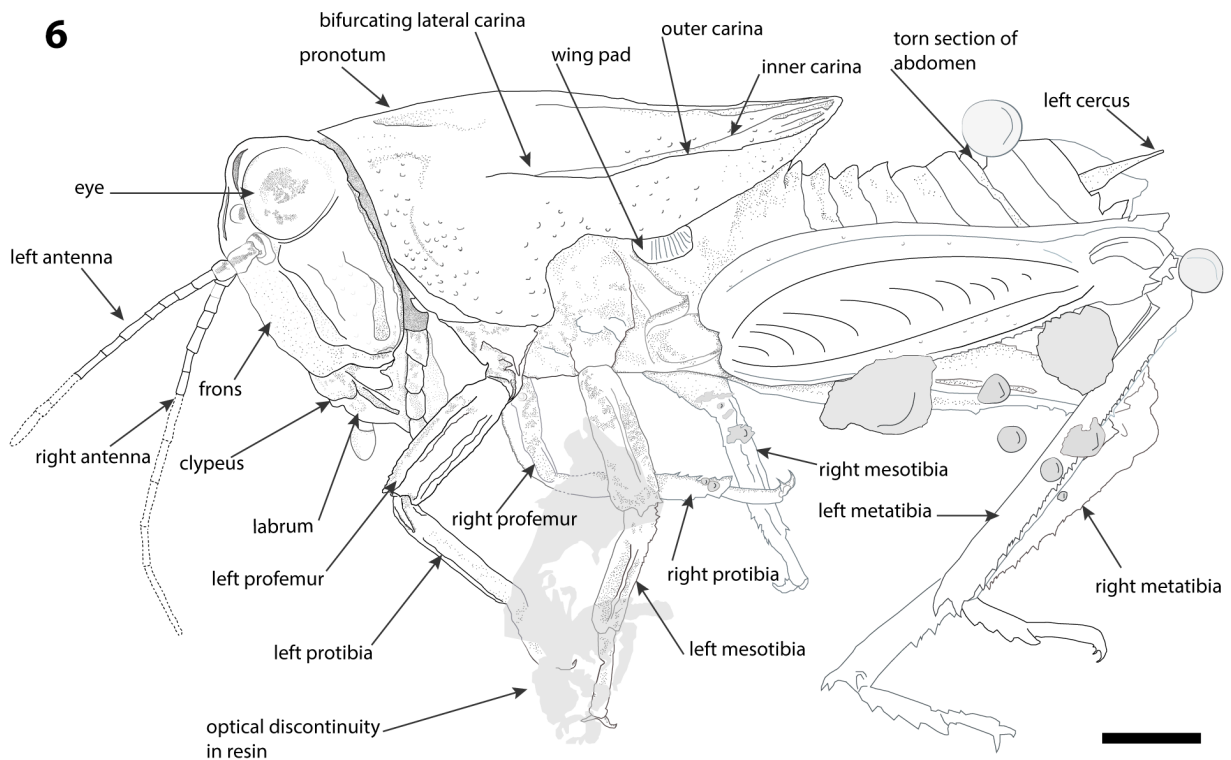
Abdomen: Abdomen c. 4.3 mm from abdominal terminus to thoracic junction. Prominent armament visible on first six abdominal tergites in the form of dorsally projected and slightly posteriorly-curved spines. Remaining tergites bare of armament. Left cercus visible, long and cone-shaped, and possessing long setae on all sides. Left paraproct visible, small and triangular. Upcurved subgenital plate. Downturned epiproct with acuminate tip.

Description of paratype (1084-5)

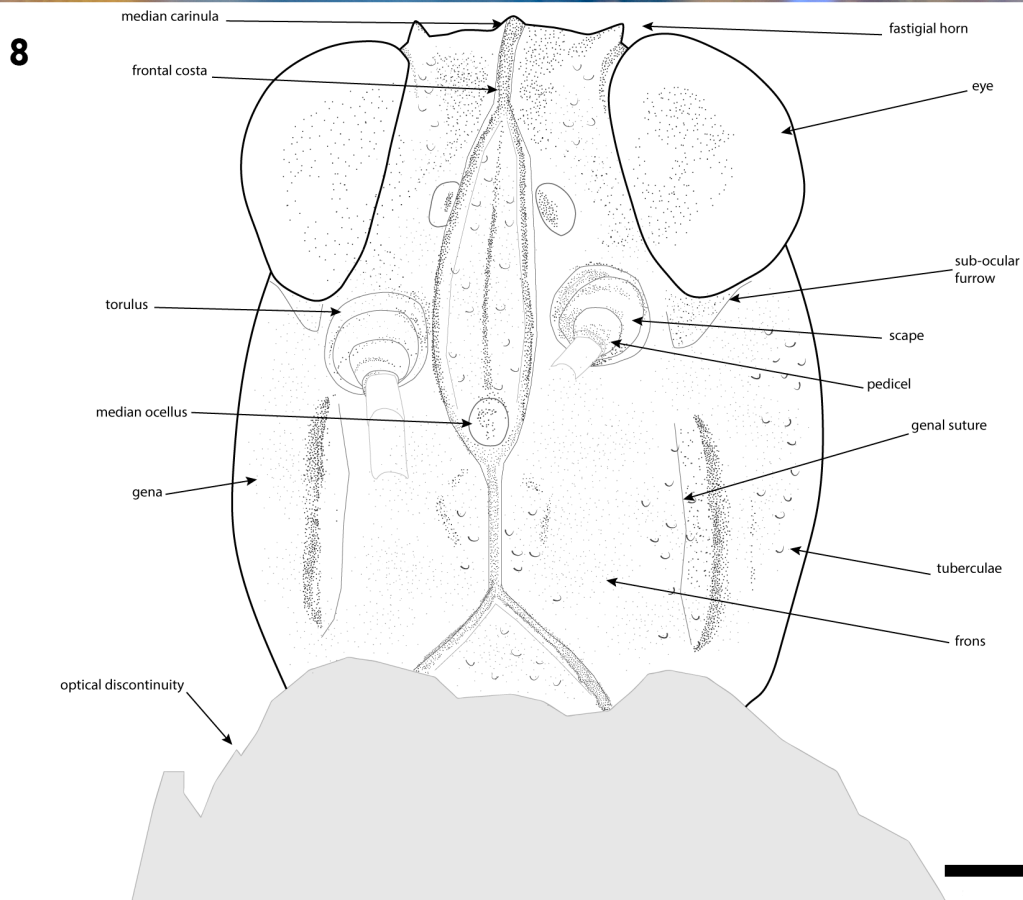
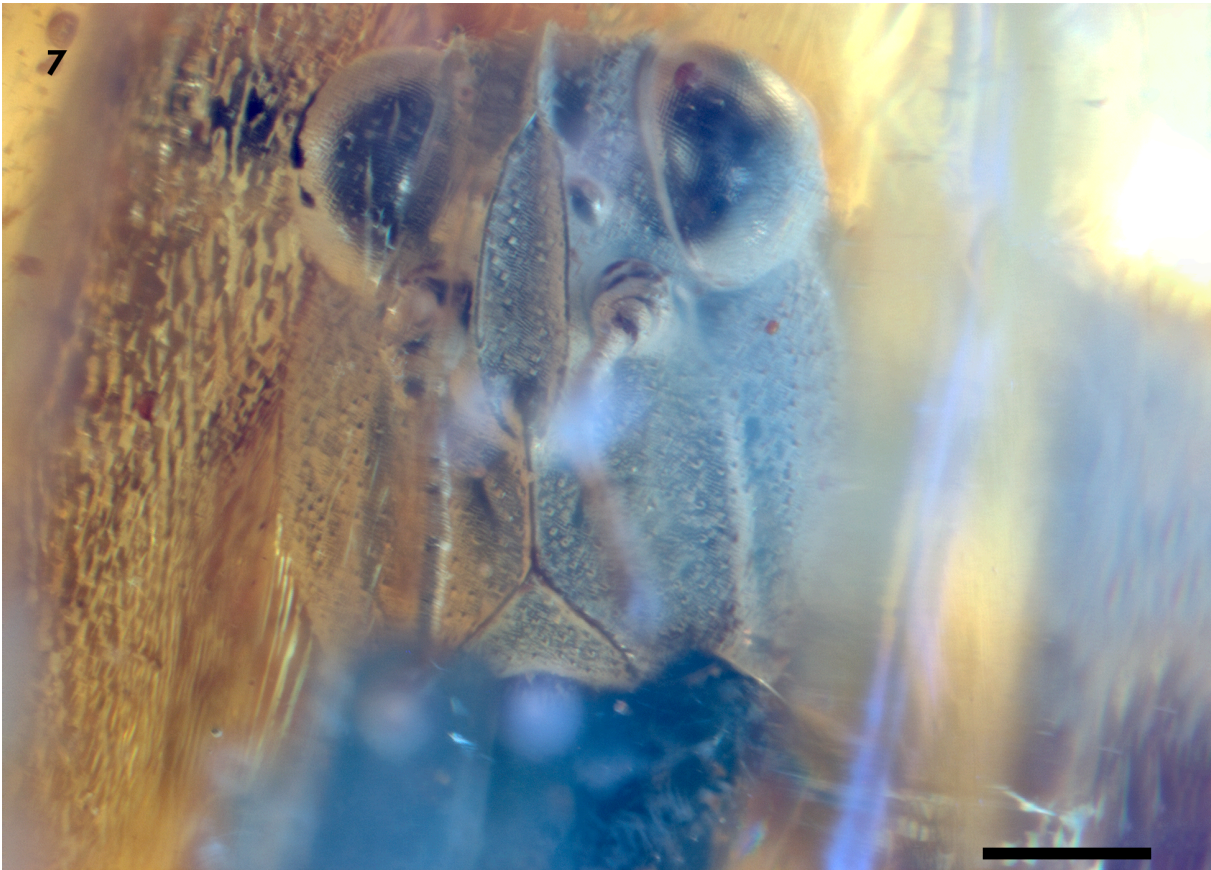
Head: Head hypognathous and dorsoventrally elongate. Integument finely granulate. Eyes globose and somewhat acutely rounded ventrally. Vertex extending slightly above eye line and projecting anteriorly just beyond eyes. Fastigial horns present, rising to just below height of the median carinula. Fovea deep and triangular. Fastigial ridge unpronounced; rounded. Median carinula weak. Frontal costa pronounced, projecting anteriorly beyond eyes, bifurcating below fastigial ridge and joins again below median ocellus. Lateral ocelli present near frontal costal bifurcation. Antennae with 20 segments including scape and pedicel. Flagellomeres two and three are shorter than antennomere one. All others relatively equal in length. Maxillary palpal segments visible and robust, but mostly obscured by forelegs and head. Labial palpal segments not visible.

Thorax: Pronotum c. 5.1 mm in length with slight anterior projection of c. 0.1 mm over the head. Posterior pronotum acuminate tip slightly upturned acuminate tip (figure 7). Median carina posteriorly low but with a sweeping rise halfway to the anterior margin before reaching roughly the height of the head vertex. Lateral carinae low-ridged along entire length from posterior apex until smoothing into the transverse sulci c. 0.2 to 0.6 mm from the left lateral anterior margin. Lateral carinae branched at c. 1.5 mm from the left lateral anterior margin of the pronotum. Lateral carinae very slight along the length of the more dorsally located branch and slightly more pronounced along the lower branch (figure 8). Humeral sinus broadly rounded and shallow. Tegminal sinus with minor rounded invagination. Lateral lobes broad and gently rounded. Pronotum cut by two sulci that cross the lateral but not the median carina. Coarsely granulate integument with larger tubercular ornament on anterior margin of pronotum near transverse sulcus. Finely granulate integument on pronotum posterior to the first transverse sulcus. Coxae robust on all legs. Trochanter thinner in pro- than meso- and metathoracic legs. Pro- and mesofemora carinate with obvious

sulcus along mesofemora. Pro- and mesofemora quadrate in cross section. Pro- and mesothoracic tibiae quadrate in cross section. Pro- and mesothoracic tibiae possess fine denticles along posterior surface. Metathoracic femora robust with wavy integument lines between lateral carinate processes. Metathoracic tibiae triangular in cross section. Ventral margin of carinate processes on foretibiae have small denticles interspersed between spines. Tibial junction with tarsi in metathoracic legs possess four spurs. Pro- and mesothoracic tarsi with three pulvilli. Metathoracic tarsi with four pulvilli, three on basitarsus and one on mid segment. Tarsi are three-segmented with two ungues and two ventral-facing unguinal setae.

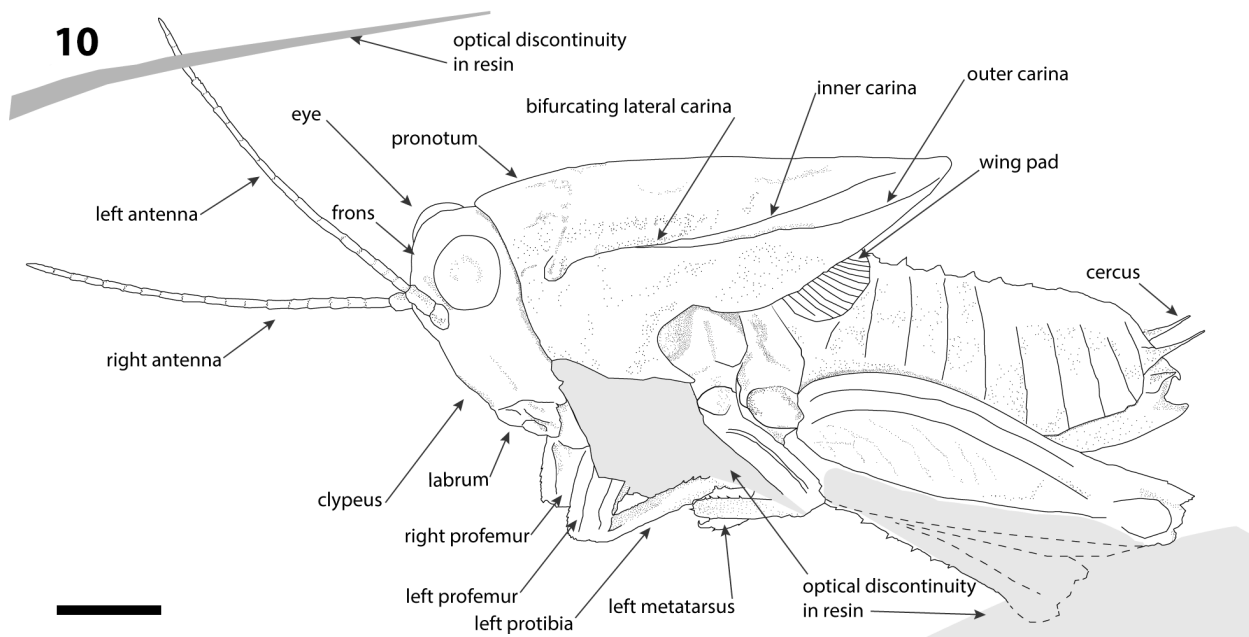


FIGURES 5–6. Fig 5. Left lateral view of paratype 1084-3 *Danatettix hoffeinsorum* early instar nymph (scale bar = 1 mm). Fig 6. Left lateral drawing of paratype 1084-3 *Danatettix hoffeinsorum* early instar nymph (scale bar = 1 mm)



FIGURES 7–8. Fig 7. Anterior view of paratype 1084-3 *Danatettix hoffeinsorum* early instar nymph (scale bar = 0.5 mm). Fig 8. Drawing of anterior view of paratype 1084-3 *Danatettix hoffeinsorum* early instar nymph (scale bar = 0.5 mm)

Abdomen: Abdomen c. 4.5 mm from tip of subgenital plate to thoracic junction. Prominent armament visible on first six abdominal tergites in the form of dorsally projected and slightly posteriorly-curved spines. Remaining tergites bare of armament. Both cerci visible, long and cone-shaped, and possessing long setae on all sides. Both paraprocts small and triangular in appearance and approximately half the length of cerci. Upcurved subgenital plate visible. Downturned epiproct visible with sharp acuminate tip.



FIGURES 9–10. Fig 9. Left lateral image of paratype 1084-5 *Danatettix hoffeinsorum* early instar nymph (scale bar = 1 mm).

Fig 10. Left lateral drawing of paratype 1084-5 *Danatettix hoffeinsorum* early instar nymph (scale bar = 1 mm)

Discussion

Because of the truncated anterior margin of the pronotum, this new taxon resembles most members of the extant Central and South American genera *Paurotarsus* and *Eutettigidea*, and is probably derived from a *Tettigidea*-like ancestor, just as may be the case in the genera *Paurotarsus* and *Paxilla* Bolívar, 1887. *Paxilla* is a monotypic genus endemic to Florida, USA, and probably represent a relict taxon that, together with *Danatettix*, suggests a greater historical diversity of the Batrachideinae in the Northern Hemisphere.

Recently described *Eotetrix unicornis* Gorochov, 2012 from the Eocene Green River Formation of Wyoming (Gorochov & Labandeira, 2012), originally not assigned to a subfamily, is also a typical batrachideine in that it possesses rectangular paranota and sharply projected anterior margin of the pronotum. *Eotetrix* is morphologically similar to *Scaria* and *Rehnidium* in that it possesses an ascending pronotal spine. The placement of *Eotetrix* in Batrachideinae implies that within the subfamily, the *Tettigidea* genus group (here tentatively defined as including *Paxilla*, *Paurotarsus*, *Tettigidea* and *Danatettix*) separated from the *Scaria* genus group (including *Scaria*, *Rehnidium* and *Eotetrix*) more than 50 million years ago.

The paleobiota of Baltic amber resembles a tropical forest ecosystem and strongly indicates a tropical paleoclimate in Europe during the Eocene (Wolfe *et al.*, 2019). Just as in most Palearctic tropical groups, Batrachideinae became extinct in Europe when the tropical forests that dominated the region disappeared. It is likely that the European tetrigid fauna underwent significant turnover as a result of multiple glaciation events in the Oligocene and Miocene during the onset of the Late Cenozoic Ice Age. Such turnover is well-documented in mammals during this period (Webb & Opdyke, 1995; Figueirido, 2012) and is almost certainly true for most organisms as environments changed during significant shifts in climate. Batrachideinae are entirely absent from Europe today, a continent inhabited by only 12 species in the genera *Paratettix* and *Tetrix* (both in the subfamily Tetriginae) (Devriese, 1996). *Danatettix* was possibly among the last batrachideines to inhabit Europe.

The paleobiota of the Baltic amber forest ecosystem has been fairly well-documented in comparison to other amber deposits (Weitschat & Wichard, 2002), and the insect fauna is known to be very diverse (e.g. Gorochov, 1989; Azar & Nel, 2008). Like the extant pygmy grasshoppers, which feed on detritus and mosses (Kuřavová *et al.*, 2016), *Danatettix* likely fed on liverworts of the family Geocalycaceae (such as *Notoscyphus balticus* Heinrichs *et al.*, 2015) and mosses of the family Mniaceae (such as *Rhizomnium dentatum* Heinrichs *et al.*, 2014), while ants (Wheeler, 1915), such as *Yantaromyrmex* (Dlussky & Dubovikoff, 2013), may have been important predators of Tetrigidae.

Acknowledgments

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