A new long-winged pygmy grasshopper in Eocene Baltic amber raises questions about the evolution of reduced tegmenula in Tetrigidae (Orthoptera)

Josip Skejo[1,2,3*], Niko Kasalo[2,3*], M. Jared Thomas[4,5*], Sam W. Heads[4*]

1 IUCN/SSC Grasshopper Specialist Group, Zagreb, Croatia.
2 SIGTET—Special Interest Group Tetrigidae, Karlsruhe, Germany.
3 University of Zagreb, Faculty of Science, Zagreb, Croatia.
4 Center for Paleontology, Illinois Natural History & State Geological Surveys, Prairie Research Institute, University of Illinois at Urbana-Champaign, 1816 South Oak Street, Champaign, Illinois 61820, USA.
5 Illinois State Geological Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, 615 East Peabody Drive, Champaign, Illinois 61820, USA.

Corresponding authors: Niko Kasalo (niko.kasalo5@gmail.com), Josip Skejo (skejo.josip@gmail.com, jskejo@biol.pmf.hr)

Academic editor: Daniel Petit | Received 18 April 2023 | Accepted 30 May 2023 | Published 9 January 2024

https://zoobank.org/1A982C52-DF7C-42FE-AD3B-376A3380829E

Citation: Skejo J, Kasalo N, Thomas MJ, Heads SW (2024) A new long-winged pygmy grasshopper in Eocene Baltic amber raises questions about the evolution of reduced tegmenula in Tetrigidae (Orthoptera). Journal of Orthoptera Research 33(1): 21–26. https://doi.org/10.3897/jor.33.105144

Abstract

Extant pygmy grasshoppers (Tetrigidae) that possess wings have the forewings reduced into scale-like tegmenula, while hind wings remain fully developed. *Rusmithia gorochovi* **gen. et sp. nov.** (Tetrigidae, Batrachideinae, Rusmithini **trib. nov.**) is described based on a single adult female holotype from Lithuanian Baltic amber, from the Bartonian-Priabonian age, some 40 million years ago, and this is the only known tetrigid in which tegmenula or tegmina (the forewings) extend as far as half the length of the hind femur. Besides this very unique trait, other characters of *Rusmithia* **gen. nov.** indicate similarity with extant and especially fossil Batrachideinae (genus *Danatettix* Thomas, Skejo & Heads, 2019). Because of the strong differences this genus and *Danatettix* have with American Batrachideinae, they are assigned to a new tribe, European Batrachideinae or Rusmithini **trib. nov.** *Acrydium bachofeni* (Zeuner, 1937) might belong to this or a sibling genus based on its very long tegmenula or *Succinotettix chopardi* Piton, 1938, based on its 19-segmented antennae; neither species is tranferred as their types could not be examined.

Keywords

Amber, autapomorphy, Baltic, European Batrachideinae, fossil, plesiomorphy, tegmina, Tetrigidae

Introduction

Although many have dedicated their lives to studying them, our knowledge of extant pygmy grasshoppers (Orthoptera, Tetrigidae) is still scarce (Cigliano et al. 2023). Given this, it is unsurprising that the available information on extinct species of the family can easily be summarized in a single table (Table 1). Such a small dataset paints a tragically incomplete picture of their evolution—a picture that is slowly being painted one fossil at a time (Sharov 1968, Thomas et al. 2019).

Most of the extant tetrigid species have fore- and hind wings. The forewings of these species are reduced to tiny scales and are called tegmenula in pygmy grasshoppers, as opposed to tegmina in winged crickets and grasshoppers. The hind wings of pygmy grasshoppers are functional and are referred to as *alae*, as in other orthopteran families (Harz 1969, Devriese 1991, 1999). The longest tegmenula have been found in †*Prototetrix* Sharov, 1968 and †*Archaeotetrix* Sharov, 1968 (Sharov 1968), although it is not clear whether they represent stem Tetrigidae or specialized Locustopsidae (Heads et al. 2014, Thomas et al. 2019). It is also not clear how long the wings were relative to body size, as the wings are the only well-preserved part of species in these genera (Sharov 1968). Because of †*Prototetrix* and †*Archaeotetrix*, it is believed that the evolution of pygmy grasshoppers included a reduction in the size of forewings (Sharov 1968).

Herein, we describe a new genus and species, †*Rusmithia gorochovi* **gen. et sp. nov.** (Batrachideinae: †Rusmithini **trib. nov.**), an extinct tetrigid from Lithuania found in Baltic amber. With tegmenula reaching the mid-portion of the hind femora, this species is the new record holder for the longest tegmenula, which makes it an invaluable snapshot of the evolutionary history of Tetrigidae.

* All the authors are of equal contribution.

Table 1. A checklist of fossil Tetrigoidea, sorted by taxonomy and approximate age, with location of the type specimens. An asterix indicates that it is unclear where the type is deposited. Updated from Thomas et al. (2019).

	CLASSIFICATION	LOCALITY	AGE
Tetrigidae: Batrachideinae: Batrachideini			
1	*Eotetrix unicornis* Gorochov, 2012	Green River Fm, Wyoming, USA	Middle Eocene
Tetrigidae: Batrachideinae: Rusmithini trib. nov.			
2	*Danatettix hoffeinsorum* Thomas, Heads & Skejo, 2019	Baltic amber	Middle Eocene
3	*Rusmithia gorochovi* gen. et sp. nov., this study	Baltic amber	Middle Eocene
Tetrigidae: Tetriginae			
4	*Eozaentetrix wittecki* Zessin, 2017	North Jutland, Denmark	Early Eocene
5	*Eozaentetrix furi* Zessin, 2017	North Jutland, Denmark	Early Eocene
Tetrigidae: Metrodorinae			
6	*Antilotettix electrum* Heads, 2009	Dominican amber	Early Miocene
7	*Baeotettix lottiae* Heads, 2009	Dominican amber	Early Miocene
8	*Electrotettix attenboroughi* Heads & Thomas, 2014	Dominican amber	Early Miocene
Tetrigidae incertae sedis			
9	*Archaeotetrix locustopseiformis* Sharov, 1968	Turga Fm, Transbaikalia, Russia	Early Cretaceous
10	*Prototetrix reductus* Sharov, 1968	Turga Fm, Transbaikalia, Russia	Early Cretaceous
11*	*Acrydium* (?) *bachofeni* (Zeuner, 1937)*	Baltic amber	Middle Eocene
12*	*Succinotettix chopardi* Piton, 1938*	Baltic amber	Middle Eocene
13*	*Tettigidea* (?) *gracilis* (Heer, 1865)*	Oeningen, Switzerland	Late Miocene

Material and methods

The holotype of *Rusmithia gorochovi* **gen. et sp. nov.** was purchased on eBay by Ru Smith who then contacted the first author. The female holotype is deposited in Ru Smith's private collection, York, UK.

The widest possible age range of Baltic amber is 25 to 43 million years (Sadowski et al. 2017), but it is currently unclear whether the younger deposits are simply redeposits of the older material, so the usual age estimate is Lutetian (47.8–41.2 Ma) to Priabonian (37.8–33.9 Ma) (Seyfullah et al. 2018), with most of the material dated to the Priabonian (Sadowski et al. 2020). We refer to our fossil as belonging to the Middle Eocene following the Lutetian–Priabonian estimates. The holotype was photographed and drawn by Ru Smith. Characters relevant for subfamily classification are number of antennal segments (>19 in Batrachideinae, <18 in other subfamilies), shape of paranota (rectangular in Batrachideinae, triangular in other subfamilies), and morphology of the legs (with sulcate dorsal margin in Batrachideinae, carinated in other subfamilies). As a result, the new genus is assigned to Batrachideinae. Taxonomy follows that of the Orthoptera species file (Cigliano et al. 2023). Morphological terminology follows Tumbrinck (2014), and nomenclature is in accordance with the International Code of the Zoological Nomenclature (ICZN 1999).

Results

Taxonomic part

Family Tetrigidae Rambur, 1838

Subfamily Batrachideinae Bolívar, 1887

Type genus.—Batrachidea Serville, 1838.

Diagnosis.—Antennae with more than 19 segments, paranota rectangular, mid-femora with sulcate dorsal margin, female spermatheca with two diverticula.

Composition.—Batrachideini (Southern and Northern America), Cassitettigini (Africa and SE Asia), Bufonidini (New Guinea, Australia, New Caledonia, and Solomon islands) (Storozhenko 2019), and Rusmithini **trib. nov.** (Eocene Europe, extinct).

Tribe Rusmithini Skejo, Kasalo, Thomas & Heads, trib. nov.

https://zoobank.org/38C79F95-AA70-452E-832D-2D2825D950D6

Diagnosis.—Antenna composed of 19 or more antennomeres. Pronotum smooth and flat. Anterior margin of the pronotum obtusely triangular, not spine-like and not projected above the head. Tegmenula and alae present. Legs elongated. Mid-femora sulcate. Genicular and antegenicular teeth of the hind femora minute, genicular notch almost indistinct.

Type genus.—Rusmithia Skejo, Kasalo, Thomas & Heads, **gen. nov.**

Composition.—Two genera (*Danatettix* and *Rusmithia*), two species. *Danatettix hoffeinsorum* Thomas, Skejo & Heads, 2019 and the herewith described *Rusmithia gorochovi* Skejo, Kasalo, Thomas & Heads, **gen. et sp. nov.** Enigmatic *Acrydium bachofeni* (Zeuner, 1937), characterized by long wings (Zeuner 1937) might also belong to this tribe as well as the genus *Succinotettix* Piton, 1938 (with one species, *S. chopardi* Piton, 1938) whose antennae are reported to have at least 19 segments (Piton 1938). However, we refrain from transferring these genera to Rusmithini as we were unable to examine the type specimens.

Genus *Rusmithia* Skejo, Kasalo, Thomas & Heads, gen. nov.

https://zoobank.org/2112E38B-6726-40EB-8AA3-6129D1CA04BD

Type species.—Rusmithia gorochovi **sp. nov.**

Diagnosis.—Antenna with 20 segments (or more, some articulations between antennomeres are not clear). Tegmenula extremely long (for a member of Tetrigidae), reaching the mid-length of the hind femur.

Composition.—A single species, *Rusmithia gorochovi* Skejo, Kasalo, Thomas & Heads, sp. nov., described herein. *Acrydium bachofeni* (Zeuner, 1937) may also belong to this genus if the long tegmenula (5 mm in length), cited in the original description, are taken into account (Zeuner 1937). However, the type of *A. bachofeni* has not been examined by us, and we are unsure of its location.

Etymology.—The new genus-group name is patronymic and honors Dr. Ru Smith, who kindly made the important specimen available to science. The name is feminine.

Rusmithia gorochovi Skejo, Kasalo, Thomas & Heads, sp. nov.

https://zoobank.org/92DD1977-586C-41E2-9024-E585BCE90B24

Figs 1 and 2

Type specimen.—**Holotype: Russian Federation** • adult female (Figs 1 and 2); Kaliningradskaya oblast', Yantarny, Anna mine; Ru Smith's collection. Syninclusions: a fly (Diptera) belonging to the family Sciaridae (det. A.J. Ross).

Etymology.—The new species name is patronymic and honours Dr. Andrei V. Gorochov, world-renowned expert on fossil Orthoptera.

Diagnosis.—As for the genus.

Description.—**Head (Fig. 2B, C, D).** In frontal view: Eyes globose. Top margin of compound eye a little above vertex. Lateral and transverse carina forming an acute angle below which surface of exoskeleton more granular; some air bubble encapsulation apparent in this part. Frontal costa prominent. Frontal costa bifurcates at approximately middle of the compound eye height. Scutellum vaguely bottle-shaped; the section between the eyes approximately as narrow as an antennal groove. Below eyes, scutellum progressively widened up to the bottom margin of the antennal groove and then progressively but slightly narrowed; section below eyes double the length of the one between the eyes. Paired ocelli placed a little above the bottom margin of the compound eye; median ocellus occluded by debris. Top margin of the antennal groove at the level of the bottom margin of the compound eye. In dorsal

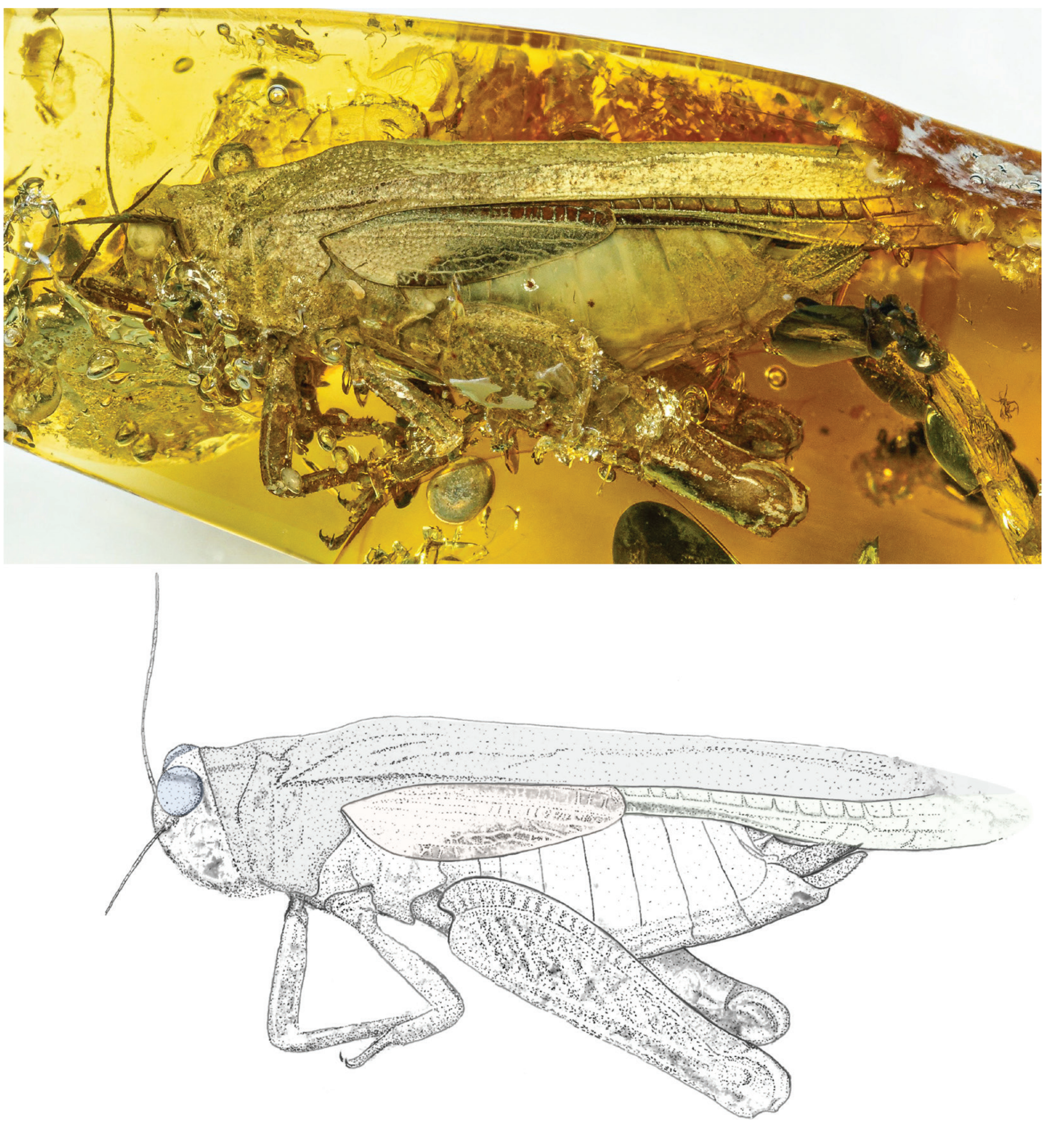

Fig. 1. *Rusmithia gorochovi* **gen. et sp. nov.** Female holotype, lateral habitus. Photo and drawing credit: Ru Smith, used with permission. Scale bar: 10 mm.

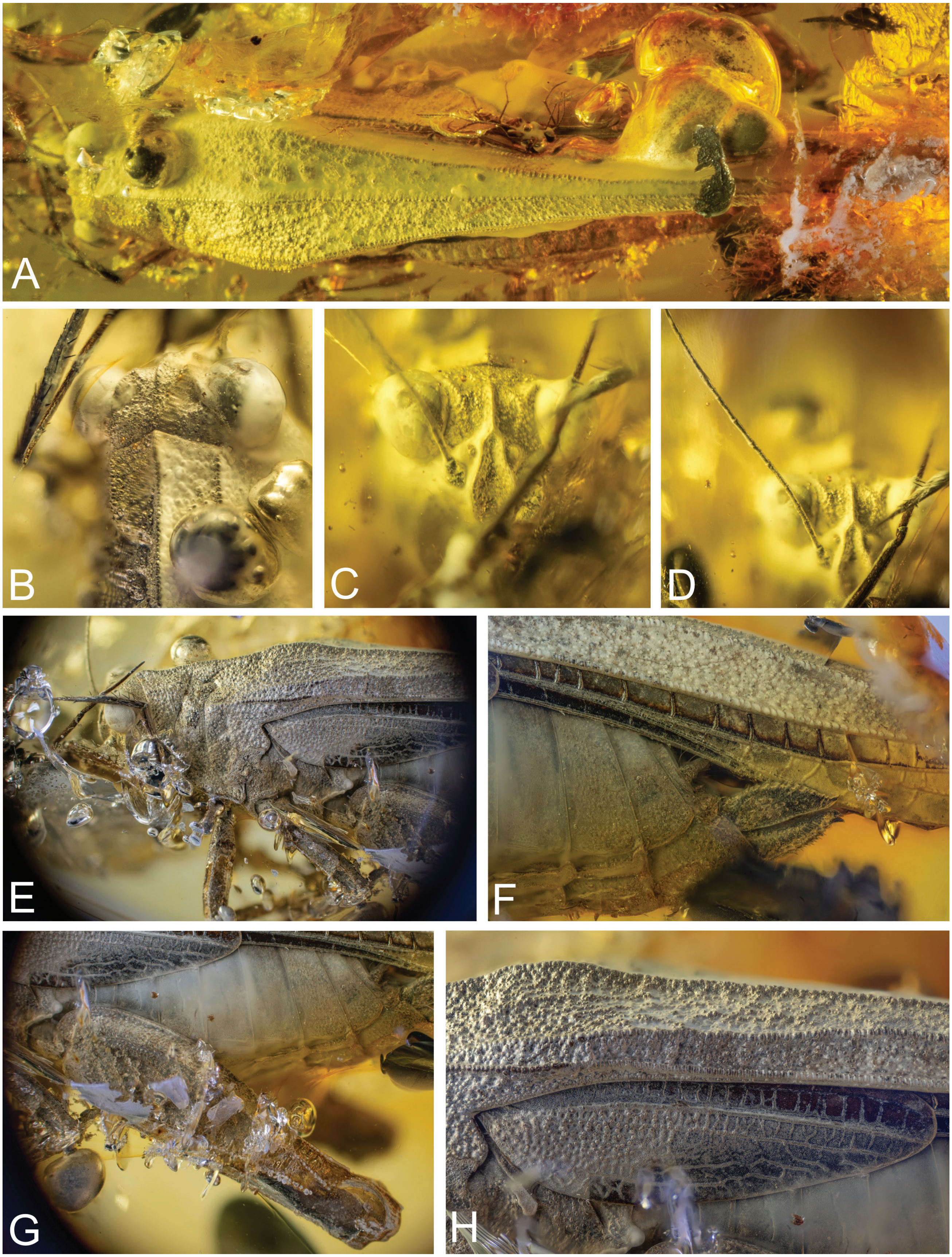

Fig. 2. *Rusmithia gorochovi* **gen. et sp. nov.**, female holotype, details. Photo credit: Ru Smith, used with permission. **A.** Dorsal view of the pronotum; **B.** Dorsal view of the head; **C.** Anterior view of the head; **D.** Antenna; **E.** Lateral view of the anterior half of the body; **F.** Ovipositor; **G.** Hind femur; **H.** Forewing.

view: Vertex highly granulated and wider than the compound eye. Anterior margin of the vertex slightly dorsal to the anterior margin of the compound eyes; frontal costa protrudes slightly anterior to the level of the compound eyes. Lateral and transverse carinae form acute triangular shapes that enclose shallow triangular fossulae. Medial carina barely visible throughout the length of the vertex. The compound eyes not touching anterior margin of pronotum. In lateral view: Frontal costa prominent. Scutellum very prominent. Most of the view obscured by encapsulated air bubbles and debris.

Pronotum (Fig. 2A, B, E). Macropronotal form. In dorsal view: Entire surface tuberculated. Anterior margin of the pronotum projected forwards in the form of an obtuse triangle. Prozonal carinae parallel. Interhumeral carinae long, converging dorsally. Median carina present throughout the length of the pronotum. Lateral area large dorsal to the tegmina.Pronotal apex occluded by debris. Wings surpass the pronotal apex but it is unclear by how much as the apex is broken. In lateral view: Paranotum rectangular. Ventral sinus in the form of an obtuse angle; tegminal sinus in the form of a nearly right angle. Infrascapular area narrow and of unclear length. Median carina forms a hump between the shoulders; anteriorly, there is a lower hump between the prozona and metazona, and the anterior process forms yet another hump, smaller than the preceding one. Dorsal to the interhumeral hump, the median carina is straight.

Wings (Fig. 2E, H). Alae well-developed, reaching past the pronotal apex. Tegmina unusually wide and long, a little less than half of the length of alae. Tegmina width more than half of that of the hind femur. Radius straight, very disctinct. Subcosta parallel to the radius. Other veins not discernable.

Legs (Fig. 2E, G). Fore- and mid-femora thin, rectangular in cross-section. Foretibiae with small teeth distally. Hind femora long and narrow with small genicular and tiny antegenicular teeth.

Ovipositor (Fig. 2F). Short, serrated. Both ovipositor valves bulging in the middle. Dorsal valve wider than ventral valve, but of same length.

Measurements.—Pronotum length 17 mm; body length 18 mm; hind femur length 9 mm; hind femur width 2 mm; tegmen length 6 mm.

Discussion

The long tegmenula of *Rusmithia gorochovi* are peculiar in that the radius and costa are clearly visible, unlike in any other known tetrigid. A similar pattern of venation can be observed in Tridactyloidea (Sharov 1968), which modern analyses have reconstructed as basal Caelifera (Song et al. 2020). This seems to imply that this morphology may be ancestral in Tetrigoidea, but such a conclusion cannot be drawn at the moment for several reasons. First, it has been shown in different taxa that reduction in wing size is a relatively common occurrence and is followed by a reduction in wing venation, with only the veins crucial for wing armature persisting (Perfilieva 2010, Žikić et al. 2017). This means that it is impossible to exclude convergence based only on the present data. Second, *Danatettix hoffeinsorum*, a European relative of *Rusmithia gorochovi*, and *Eotetrix unicornis*, an American fossil Batrachideinae, both have typical tetrigid tegmenula (Gorochov and Labandeira 2012, Thomas et al. 2019), which casts doubt on the continuous persistence of this morphology through time. *Acrydium* (?) *bachofeni* is stated as having long tegmenula by Zeuner (1937), meaning that it could belong to *Rusmithia* or a new closely related genus. Examining the type of this species would help elucidate the taxonomy of European Batrachideinae and the evolution of tegmina in this group. Third, *Archaeotetrix* and *Prototetrix*, which are much older than *Rusmithia*, also exhibit long tegmenula but with different venation (Sharov 1968), although their affinities remain obscure. The most parsimonious explanation is that *Rusmithia* belongs to a line of Batrachideinae in which the longer tegmenula were retained, which may represent an intermediary state between the fully winged ancestral form and the more modern, reduced forms. This implies the possibility that tegminal reduction occurred at least twice in Tetrigoidea. More research is needed to clarify the evolution of Tetrigoidea and their wings.

Baltic amber is a gold mine for fossil arthropods (Weitschat and Wichard 2010), comparable to the number of plant taxa described from the same deposits (Sadowski et al. 2020). A recent botanical study by Sadowski et al. (2020) revealed the presence of various habitats in the Baltic region, ranging from coastal swamps to mixed mesophytic conifer-angiosperm forests with a wide range of transitional habitats between them. Similar habitats are found today in the warm-temperate regions of East Asia and North America, and they house numerous species of modern Tetrigidae, including Batrachideinae (Cigliano et al. 2023). Thus, with relative certainty, we can conclude that *Rusmithia gorochovi* likely spent its time in warm and wet habitats feeding on algae, mosses, and detritrus in unknown proportions (Hochkirch et al. 2000, Kuřavová et al. 2020). The fly trapped together with the holotype of *R. gorochovi* (Fig. 3) belongs to the family Sciaridae (det. Andrew Ross), which feed on detritus and fungi (Gerhardt and Hribar 2019), indicating their shared habitat.

The fossil record of Tetrigidae is scant, and much more work needs to be done. Most notably, the placement of *Archaeotetrix locustopseiformis* and *Prototetrix reductus* within the taxonomy of Tetrigoidea is unclear (Sharov 1968, Thomas et al. 2019), if they indeed belong to this superfamily. Because the venation of the tegmina of these species differs from both the extant and other known extinct tetrigids, it should be closely examined as it could indicate that these two species are only distantly related to the other known tetrigids. Furthermore, the types of *Acrydium* (?) *bachofeni*, *Succinotettix chopardi*, and Heer's (1856) *Tettigidea* (?) *gracilis* could not be examined, and their affinities remain unclear. If and when they are found, they will undoubtedly shed much-needed light on the evolutionary history of Tetrigidae.

Fig. 3. A fly belonging to the family Sciaridae, encapsulated together with *Rusmithia gorochovi* **gen. et sp. nov.**

Acknowledgements

We are infinitely grateful to Ru Smith who purchased the specimen and made it available for scientific description, took many photographs of the holotype, and made the drawing included herein. We thank the Orthopterists' Society for their support in publishing this article.

References

Cigliano MM, Braun H, Eades DC, Otte D (2023) Orthoptera Species File. Version 5.0/5.0. http://orthoptera.speciesfile.org [Accessed on 23.1.2023]

Devriese H (1991) Contribution à l'étude des Tetrigidae de Madagascar (Orthoptera). Bulletin et Annales de la Société Royale Belge d'Entomologie 127: 119–131.

Devriese H (1999) Revision des Xerophyllini d'Afrique (Orthoptera, Tetrigidae). Belgian Journal of Entomology 1: 21–99.

Gerhardt RR, Hribar LJ (2019) Flies (Diptera). In: Mullen GR, Durden LA (Eds) Medical and veterinary entomology. Elsevier Academic Press, Cambridge, Massachusetts, 171–188. https://doi.org/10.1016/B978-0-12-814043-7.00011-X

Gorochov AV, Labandeira CC (2012) Eocene Orthoptera from Green River Formation of Wyoming (USA). Russian Entomological Journal 21: 357–370. https://doi.org/10.15298/rusentj.21.4.02

Harz K (1969) The Orthoptera of Europe I. In: Junk W (Ed.) Series Entomologica. Vol. 5. Publishers, The Hague, 1–749. https://doi.org/10.1007/978-94-017-2511-8

Heads SW, Thomas MJ, Wang Y (2014) A remarkable new pygmy grasshopper (Orthoptera, Tetrigidae) in Miocene amber from the Dominican Republic. ZooKeys 429: 87–100. https://doi.org/10.3897/zookeys.429.8020

Heer O (1865) Die Urwelt der Schweiz. Schulthess, Zurich, 622 pp.

Hochkirch A, Gröning J, Loos T, Metzing C, Reichelt M (2000) Specialized diet and feeding habits as key factors for the habitat requirements of the grasshopper species *Tetrix subulata* (Orthoptera: Tetrigidae). Entomologia generalis 25: 39–51. https://doi.org/10.1127/entom.gen/25/2000/39

ICZN [International Commission on Zoological Nomenclature] (1999) International code of zoological nomenclature. Fourth Edition. London: The International Trust for Zoological Nomenclature.

Kuřavová K, Šipoš J, Kočárek P (2020) Energy balance of food in a detrito bryophagous groundhopper (Orthoptera: Tetrigidae). PeerJ 8: e9603. https://doi.org/10.7717/peerj.9603

Perfilieva KS (2010) Trends in evolution of ant wing venation (Hymenoptera, Formicidae). Entomological Review 90: 857–870. https://doi.org/10.1134/S0013873810070043

Piton L-E (1938) *Succinotettix chopardi* Piton, orthoptère (Tetricinae) inédit de l'ambre de la Baltique. Bulletin de la Société Entomologique de France 43: 226–227. https://doi.org/10.3406/bsef.1938.15319

Sadowski E-M, Schmidt AR, 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, Seyfullah LJ, Wilson CA, Calvin CL, Schmidt AR (2017) Diverse early dwarf mistletoes (Arceuthobium), ecological keystones of the Eocene Baltic amber biota. American Journal of Botany 104: 694–718. https://doi.org/10.3732/ajb.1600390

Serville A (1838) Histoire Naturelle des Insectes. Orthoptères. Librairie encylopédique de Roret, Paris, 776 pp.

Seyfullah LJ, Beimforde C, Dal Corso J, Perrichot V, Rikkinen J, Schmidt AR (2018) Production and preservation of resins–past and present. Biological Reviews 93: 1684–1714. https://doi.org/10.1111/brv.12414

Sharov AG (1968) Filogniya orthopteroidnykh nasekomykh [1971 English translation: Phylogeny of the Orthopteroidea]. Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR [= Transactions of the Institute of Paleontology, USSR Academy of Sciences] 118: 1–216.

Song H, Béthoux O, Shin S, Donath A, Letsch H, Liu S, McKenna DD, Meng G, Misof B, Podsiadlowski L, Zhou X, Wipfler B, Simon S (2020) Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. Nature Communications 11: 4939. https://doi.org/10.1038/s41467-020-18739-4

Storozhenko SY (2019) New taxa of pygmy grasshoppers from Australia with notes on classification of the subfamily Batrachideinae (Orthoptera: Tetrigidae). Zoosystematica Rossica 28: 94–107. https://doi.org/10.31610/zsr/2019.28.1.94

Thomas MJ, Skejo J, Heads SW (2019) The last batrachideine of Europe: A new genus and species of pygmy grasshopper (Orthoptera: Tetrigidae) from Eocene Baltic amber. Zootaxa 4686: 435–445. https://doi.org/10.11646/zootaxa.4686.3.9

Tumbrinck J (2014) Taxonomic revision of the Cladonotinae (Orthoptera: Tetrigidae) from the islands of South-East Asia and from Australia, with general remarks to the classification and morphology of the Tetrigidae and descriptions of new genera and species from New Guinea and New Caledonia. In: Telnov D (Ed.) Biodiversity, Biogeography and Nature Conservation in Wallacea and New Guinea (Vol. II). The Entomological Society of Latvia, Riga, 345–396.

Weitschat W, Wichard W (2010) Baltic Amber. In: Penney D (Ed.) Biodiversity of fossils in amber from the major world deposits. Siri Scientific Press, Manchester, 80–115.

Zessin W (2017) Neue Insekten aus dem Moler (Paläozän/Eozän) von Dänemark Teil 3 (Orthoptera: Caelifera: Eumastacidae, Tetrigidae). Virgo 19: 77–83.

Zeuner FE (1937) Descriptions of new genera and species of fossil Saltatoria (Orthoptera). Proceedings of the Royal Entomological Society of London (B) 6: 154–159. https://doi.org/10.1111/j.1365-3113.1937.tb00314.x

Žikić V, Stanković SS, Petrović A, Ilić Milošević M, Tomanović Ž, Klingenberg CP, Ivanović A (2017) Evolutionary relationships of wing venation and wing size and shape in Aphidiinae (Hymenoptera: Braconidae). Organisms Diversity & Evolution 17: 607–617. https://doi.org/10.1007/s13127-017-0338-2