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Two new fossil Tetrigidae (Insecta: Orthoptera: Caelifera) from the Grube Messel (Germany)

Niko Kasalo¹ · Josip Skejo² · Josef Tumbrinck³ · Sonja Wedmann⁴ · Martin Husemann⁵

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Abstract

The Grube Messel is an important Fossillagerstätte in Germany and has a high importance because of the excellently preserved specimens, especially in terms of insects. So far no Orthoptera from the Eocene of Grube Messel have been described. To change this, here we describe two new genera and species of Tetrigidae: *Messeltettix cryptoantennatus* gen. et sp. nov. and *Archaeoarmatus messelensis* gen. et sp. nov. We make suggestions on the systematic position of these species and discuss their meaning for our understanding of the evolution of this interesting family of grasshoppers.

Keywords Batrachideinae · Fossil insect · Eocene · Grouse hopper · Pygmy hopper

Introduction

Tetrigidae is a group of grasshoppers characterised by a relatively small size and an extended pronotum. Currently, about 2000 extant species are known (Cigliano et al. 2024). However, their fossil record is scarce. So far only 12 fossil species have been described: *Antillotettix electrum* Heads,

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 Sonja Wedmann sonja.wedmann@senckenberg.de
Martin Husemann

martin.husemann@smnk.de

- ¹ Laboratory of Evolutionary Genetics, Ruder Bošković Institute, Bijenička cesta 54, HR-10000 Zagreb, Croatia
- ² Faculty of Science, Department of Biology, Evolution Lab, University of Zagreb, Horvatovac 102a, 10000 Zagreb, Croatia
- ³ Wassenberg, Germany
- ⁴ Senckenberg Forschungsstation Grube Messel, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Markstraße 35, 64409 Messel, Germany
- ⁵ Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstraße 13, 76133 Karlsruhe, Germany

2009, Baeotettix lottiae Heads, 2009 and Electrotettix attenboroughi Heads and Thomas, 2014 (in Heads et al. 2014) from Dominican amber; Archaeotetrix locustopseiformis Sharov, 1968 and Prototetrix reductus Sharov, 1968 from Russia; Danatettix hoffeinsorum Thomas, Skejo and Heads, 2019, Rusmithia gorochovi Skejo, Kasalo, Thomas and Heads, 2024, Succinotettix bachofeni (Zeuner, 1937) and S. chopardi Piton, 1938 from Baltic amber; Eotetrix unicornis Gorochov, 2012 from the Green River formation of North America; and Eozaentetrix furi Zessin, 2017d and E. wittecki Zessin, 2017 from Denmark. These fossil Tetrigidae stretch across large geographic areas and several subfamilies: while many are not assigned to a subfamily, B. lottiae, E. attenboroughi and A. electrum are considered part of Metrodorinae (Kasalo et al. 2023c), D. hoffeinsorum and R. gorochovi are considered part of Batrachideinae: Rusmithini (Skejo et al. 2024), E. unicornis is part of Batrachideinae: Batrachideini, and S. bachofeni and S. chopardi are tentatively part of Tetriginae (Cigliano et al. 2024).

Here, we describe two new species of fossil Tetrigidae from the German Fossillagerstätte Grube Messel. The Messel pit fossil site is a UNESCO World Heritage which is located some 30 km south of the city Frankfurt am Main and is renowned for the high quality of preservation of its fossils (e. g. Smith et al. 2018). The fossiliferous sediments are lacustrine 'oil shales' which formed in a former maar lake (Schulz et al. 2002; Felder and Harms 2004) in the Eocene, between ca. 48.06 and 47.22 million years ago (Kaboth-Bahr et al. 2024). Among currently more than 20 000 fossil invertebrates from Messel in the Senckenberg collection, only three specimens could be identified as Tetrigidae.

Materials and Methods

Three fossil specimens of Tetrigidae were unearthed at Grube Messel (49.9186, 8.7581) in Hesse, Germany. The specimens are deposited in the collection of Messel invertebrate fossils of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (SF), Germany, located at the Senckenberg Forschungsstation Grube Messel, under the collection numbers SF-MeI00684, SF-MeI01665 and SF-MeI20610. Specimen SF-MeI00684 was collected in the year 1984 at digging site 5 (grid square E15), in layers near local marker horizon alpha. Specimen SF-MeI01665 was collected in 1986 at digging site 29 (grid square H12/13) in layers near local marker horizon M. Specimen SF-MeI20610 was collected in 2022 in grid square F9, in quadrant Q14, in layers between 1.97m to 2.29m above local marker horizon alpha. The specimens are conserved in glycerine to prevent destruction by desiccation.

Imaging was done with either a Leica MZ12.5 stereomicroscope with an attached Nikon D300 digital camera or with a Leica M165 C stereomicroscope with an attached digital camera Jenoptik Progress Gryphax. Measurements were taken using ImageJ 1.53t (Schneider et al. 2012). The following measurements were taken: Antenna length—AL; Head length—HL; Body length—BL; Anterior femur length— AFL; Middle tibia length—MTL; Hind femur length—HFL; Hind tibia length—HTL; Ovipositor length—OL; Tegmen length—TL; First hind tarsal segment length—FHTL; Third hind tarsal segment length—THTL. Since all of the specimens reported here were preserved at an angle, these measurements are approximate. All measurements are given in mm.

Results

Systematic palaeontology

Order Orthoptera Olivier, 1789 Superfamily Tetrigoidea Rambur, 1838 Family Tetrigidae Rambur, 1838 Subfamily Batrachideinae Bolívar, 1887 Tribe Rusmithini Skejo, Kasalo, Thomas and Heads, 2024

Messeltettix gen. nov. zoobank.org:act:49922E09-F944-433B-A71D-DE6E-CA6C41A3

Type species: Messeltettix cryptoantennatus sp. nov.

Etymology: The genus is named after the Fossillagerstätte Grube Messel with the suffix "-tettix", common for many Tetrigidae genera. The genus name is of masculine gender.

Diagnosis of genus: Inseparable from the specific diagnosis.

Messeltettix cryptoantennatus sp. nov. (Figs. 1–2) zoobank.org:act:576FEFE5-EC3D-4EE2-AD24-83741856D084

Holotype specimen ID: SF-MeI20610 (Fig. 1) Paratype specimen ID: SF-MeI00684 (Fig. 2)

Etymology: The species is named after the antennae which are conserved but segments cannot be clearly differentiated. **Type locality and type horizon**. Grube Messel, Hesse, Germany; middle Messel Formation, early middle Eocene: Geiseltalian.

Diagnosis: Antennal grooves at level of bottom margin of eyes. Antennae long and filiform. Anterior margin of pronotum with a slight spine. Median carina of pronotum elevated in anterior quarter of pronotum. Long first tarsal segments of anterior and middle legs. Relatively long tegmina, exceeding the length of hind tarsus. Third hind tarsal segment much shorter than first.

Description of holotype

General remarks: The specimen is preserved in a way that exposes its right lateral profile. The abdomen is preserved, revealing a structure strongly resembling an ovipositor, suggesting an adult female.

Head (Fig. 1a, d): Separated from the body, only right lateral profile visible. Frontal costa roundly protruding in front of the anterior margin of eyes. Midline of antennal grooves approximately at the bottom margin of eyes. Antennae filiform, but not well preserved.

Pronotum (Fig. 1a): Macropronotal. Pronotal apex invisible. Median carina elevated in the anterior quarter of pronotum, forming low and straight elevation. Anterior margin of pronotum forming a short spine. Lateral lobes indistinguishable.

Wings (Fig. 1a, c): Tegmen preserved, relatively long, exceeding the length of hind tarsus.

Legs (Fig. 1a, b): Left fore femur preserved, imprinted diagonally, apparently smooth. Hind femur preserved, apparently smooth, genicular and antegenicular teeth not clearly discernable, likely due to their small size. Hind tibia preserved, long and smooth, with small spines in distal half. Hind tarsus preserved, third segment much shorter than first.

Measurements: HL 1.7; BL 12.9; HFL 6.1; HTL 5.7; OL 1.6; TL 2.9; FHTL 1.00 THTL 0.5



Fig. 1 Holotype specimen of *Messeltettix cryptoantennatus* sp. nov., SF-MeI20610. **a** Full lateral view. **b** Hind tibia with tarsi. **c** Front wing. **d** Head with antennae. All scale bars equal 1 mm

Description of paratype

General remarks: The specimen is preserved in a way that exposes its left lateral profile. Adult. The abdomen is preserved, but the sex is indistinguishable. Considering that this specimen is smaller than the female holotype (see measurements), it is possible that this one is male.

Head (Fig. 2a, b): Separated from the body, only left lateral profile visible. Frontal costa roundly protruding in front of the anterior margin of eyes. Midline of antennal grooves approximately at the bottom margin of eyes. Antennae long and filiform. Antennomeres uncountable; potentially 17–19, estimated by length.

Pronotum (Fig. 2a, c): Macropronotal. Pronotal apex invisible. Median carina elevated in the anterior quarter

of pronotum, forming low and straight elevation. Anterior margin of pronotum forming a short spine. Lateral lobes indistinguishable.

Legs (Fig. 2a, d): Anterior femora preserved, right one visible in profile. Fore femur robust with slightly wavy margins, but unclear if the entire right femur is preserved. Fore tibia preserved, straight and smooth. First segment of fore tarsus preserved, apparently long. Middle tibia preserved, slightly expanded in distal half. Middle tarsus preserved, long first segment and claw. Hind femur preserved, apparently smooth, genicular and antegenicular teeth invisible. Hind tibia preserved, long and smooth.

Measurements: AL 5.8; HL 1.3; BL 9.9; MTL 2.1; HFL 5.1; HTL 4.1.



Fig. 2 Paratype specimen of *Messeltettix cryptoantennatus* sp. nov., SF-MeI00684. **a** Whole lateral view. **b** Head with antennae. **c** Pronotum. **d** Middle legs. All scale bars equal 1 mm

Notes: The number of antennomeres is an important diagnostic character at the level of subfamily. The fossilisation process did not preserve any clear breaks between the antennomeres in the paratype, making a definitive count impossible. However, by measuring segments that could possibly represent antennomeres (defined by abrupt changes in colouration or width in the fossilised antenna) and dividing the total length of the antenna by the average length of an antennomere, we can estimate the number of 17–19 antennomeres. Depending on the way measures are taken, this number can vary even further, but it seems

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to be relatively high, implying that the present specimen belongs to Batrachideinae. Further proof of this categorization stems from the presence of an anterior pronotal spine and the apparently long first tarsal segment of the fore and middle leg. Some Tetriginae, such as certain species of *Hedotettix* Bolívar, 1887, have the anterior margin of pronotum expressed in the form of a triangular protrusion, but never in the form of a clear spine. The tegmen in the holotype is relatively long in comparison to many modern tetrigids. This feature supports the classification under Batrachideinae: Rusmithini. Subfamily Batrachideinae Bolívar, 1887 Tribe Batrachideini Bolívar, 1887 Archaeoarmatus gen. nov. zoobank.org:act:A10E942C-79CF-4FAD-B490-1438DC39A9AB

Type species: Archaeoarmatus messelensis sp. nov.

Etymology: The genus name is composed of the prefix "archaeo-", meaning "ancient" and –"armatus", which is the perfect passive participle of the Latin verb armō, meaning "armed, equipped" The genus name is of masculine gender and refers to the anterior pronotal spine observed in this genus. **Diagnosis of genus:** Inseparable from the specific diagnosis.

Archaeoarmatus messelensis sp. nov. (Fig. 3) zoobank.org:act:39B1B008-05E8-4CD7-AD0B-5245C7EC4819 **Etymology:** The species is named after the location where it was found, the Fossillagerstätte Grube Messel.

Type locality and type horizon: Grube Messel, Hesse, Germany; middle Messel Formation, early middle Eocene: Geiseltalian.

Diagnosis: Wide dome-like vertex. Pronotum mostly flat, forming a long anterior spine (distinguishable in Fig. 3 by the notch directly above the anterior margin of the visible left eye, which we interpret as the separating area between the head and the spine). Long first tarsal segments of fore and middle legs. Slim hind femur.

Description of holotype

General remarks: The specimen is preserved at an angle that partially exposes its dorsal and left lateral aspects with



Fig. 3 Holotype specimen of Archaeoarmatus messelensis sp. nov., SF-MeI01665. **a** Whole lateral view. **b** Head with antennae. **c** Middle legs. **d** Remains of pronotum. All scale bars equal 1 mm

its frons oriented a little away from the fossilisation plane. Adult, likely female.

Head (Fig. 3a, b): Vertex seemingly wide and dome like, its highest point decidedly above the top margin of eyes. Antennae only partially preserved.

Pronotum (Fig. 3a, d): Macropronotal. Pronotal apex not preserved, seemingly reaching close to the tip of alae. Pronotal surface seemingly flat, without significantly elevated median carina—the hump visible above prozona is likely the right humeral angle that is visible due to the angle of imprinting. Anterior margin of pronotum forming a long spine that extends above the head.

Legs (Fig. 3a, c): Left anterior leg preserved almost completely, imprinted diagonally; femur and tibia smooth; first tarsal segment long. Left middle leg preserved almost completely, but overlaps with other structures; femur potentially expanded (or overlapping with other structures); tibia smooth and a little expanded in the middle; first tarsal segment long. Posterior left femur partially preserved; long and slim.

Measurements: HL 1.6; BL 10.5; AFL 2.3; MTL 2.1; OL 1.0.

Notes: The dome-like vertex in anterior view coupled with a strong anterior spine of the pronotum undoubtedly places this species in the subfamily Batrachideinae. Many important diagnostic characters are invisible, but the species seems to generally resemble the extinct *E. unicornis*, and by extension many extant Batrachideini members.

Discussion

We interpret the two fossil tetrigid species from Grube Messel as representatives of two different tribes of Batrachideinae, the earliest tetrigid subfamily (Song et al. 2015). Messeltettix gen. nov. fits with the members of the tribe Rusmithini due to its slight anterior spine of the pronotum, the seemingly low placement of antennal grooves, and relatively large tegmina (Skejo et al. 2024). Rusmithini members are currently known only from European Eocene fossils, that is, from Baltic amber (Skejo et al. 2024), and from Grube Messel (this study). On the other hand, Archaeoarmatus gen. nov. resembles Eotetrix unicornis, an fossil known from the Green River Formation (middle Eocene), Wyoming, USA (Gorochov and Labandeira 2012). This species is traditionally classified under the tribe Batrachideini due to its general similarity with some of that tribe's species, e.g. Tettigidea armata species group (Kasalo et al. 2023b).

However, neither of the herein described specimens is preserved in a way that undoubtedly shows their facial features, which are indispensable for higher taxonomy and thus makes it impossible to confidently classify them. The situation is complicated by the fact that not even the extant Batrachideinae have been revised (Kasalo et al. 2023b). Rusmithini and Batrachideini (defined around Batrachidea and genera such as *Tettigidea* and *Scaria*) differ significantly in their facial morphologies, but there are genera such as Paurotarsus, Procellator, Naskreckiana, and Halmatettix that do not fit neatly into this system. Most notably, the facial morphologies of Naskreckiana and Halmatettix appear to be intermediate between those of Rusmithini and Batrachideini, while the short third hind tarsal segment in Paurotarsus, particularly P. ruficornis (Walker, 1871) and P. pennatulus Itrac-Bruneau and Doucet, 2023, strongly resembles that observed in Messeltettix gen. nov. Problems such as this first need to be resolved, preferably with the help of molecular data, before more concrete hypotheses about the extinct Batrachideinae can be made. For example, the phylogenetic analysis of the COI marker of some Batrachideini does not suggest a close relationship of Paurotarsus together with other Batrachideini (Kasalo et al. 2023a). Therefore, it is possible that there are multiple distinct lineages grouped under Batrachideini. Many if not all of these potential lineages of Batrachideinae could have already been present in Laurasia prior to its breakup into North America and Eurasia (Correia and Murphy 2020). The Cenozoic cooling in Europe most likely led to the complete extinction of this group on that continent (Skejo et al. 2024). It would thus not be surprising if a true member of Batrachideini would be discovered fossilised in the Eocene of Europe.

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Data availability The specimens are stored in the collection of Messel fossils of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (SF), Germany, division Messel Research and Mammalogy. The collection of the invertebrate fossils from Messel is specifically located at the Senckenberg Forschungsstation Grube Messel.

Declarations

Conflict of interest SW is guest editor of the special issue on "Pre-Quaternary maar/volcanogenic lakes as Konservat Lagerstätten— Messel and beyond." of the journal *Palaeobiodiversity and Palaeoenvironments*. She was not involved in the peer review and decision process for this contribution. All other authors declare that they have no conflict of interest. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

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