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Upper Liassic Amphiesmenopterans (Trichoptera + Lepidoptera) from Germany – a review

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Abstract. Amphiesmenopterans are represented in the Lower Toarcian marine insect taphocoenoses of Germany by stem group members (*Necrotaulius* HANDLIRSCH, 1906, *Mesotrichopteridium* HANDLIRSCH, 1906). Female terminalia of *Necrotaulius* resembling the ovipositor indicate that these insects laid their eggs rather in soil than in water. One species of genuine Trichoptera (*Liadotaulius* HANDLIRSCH, 1939) exhibited sexual dimorphism. At least two species of Lepidoptera related to Micropterygidae were found.

Key words: Amphiesmenoptera, Trichoptera, *Liadotaulius*, *Oncovena*, Necrotauliidae, *Necrotaulius*, *Mesotrichopteridium*, Grylloblattida, Prosepididontidae, *Prosepididontus*, Diptera, Hennigmatidae, *Metatrichopteridium*, Lepidoptera, Mesozoic, Jurassic, Lower Toarcian, Germany.

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I. INTRODUCTION

After the revision of 35 "trichopteran" types described by GEINITZ (1880, 1884) and HANDLIRSCH (1906, 1920, 1939) from the Lower Toarcian of Dobbertin and the reevaluation of types described by BODE (1905, 1953) and TILLYARD (1933) from the Lower Toarcian of Braunschweig and England it is now possible to give a more precise picture of the systematics and distribution of the amphiesmenopterans in the Lower Jurassic marine insect taphocoenoses of Germany (ANSORGE 2002). All these insects, except *Prosepidontus calopteryx* HANDLIRSCH 1920, were described within the family Necrotauliidae HANDLIRSCH 1906, which turned out to be a waste basket, containing representatives of different insect orders. New and well preserved material from several other German Lower Toarcian localities: Grimmen (Western Pomerania), Schandelah near Braunschweig (Lower Saxony), Kerkhofen (Bavaria), Holzmaden (Württemberg) was studied for comparison with the type material.

D e p o s i t o r y. The specimens figured here are housed in the following collections: FGWG, Institut für Geologische Wissenschaften der Ernst-Moritz-Arndt-Universität Greifswald; MB.I. Museum für Naturkunde der Humboldt Universität Berlin; LGA, LDA, ANSORGE collection, later to be housed at Museum für Naturkunde der Humboldt Universität Berlin.

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II. AMPHIESMENOPTERANS: LAST REVISIONS SUMMARIZED

Prosepididontus calopteryx HANDLIRSCH, 1920 (Fig. 2A) was transferred from Trichoptera to Grylloblattida: Geinitziidae. The anal loop, like structure of *Prosepididontus calopteryx*, is built of the concave CuP and two anal veins, therefore the species has nothing in common with amphiesmenopterans. Prosepididontidae HANDLIRSCH, 1920, established for the type species, was synonymized under Geinitziidae HANDLIRSCH, 1906 (ANSORGE & RASNITSYN 2000).

Metatrichopteridium confusum HANDLIRSCH, 1939 (Fig. 2B) is a dipteran (Diptera: Hennigmatidae) and represents the oldest fossil record of this archaic family (ANSORGE 2001).

After my revision of the Upper Liassic necrotauliids (ANSORGE 2002) the genus *Necrotaulius* HANDLIRSCH, 1906 now contains only one species, *Necrotaulius parvulus* (GEINITZ, 1884) with eight synonymized species, (Fig. 1A, 2C-E; Appendix). *Necrotaulius intermedius* HANDLIRSCH, 1906 (Fig. 1B-C, 2F-G) with six synonymized species (Appendix) was transferred to *Mesotrichopteridium* HANDLIRSCH, 1906 (= *Mesotrichopteridium intermedium*). *Prorhyacophila* RIECK, 1955 from the Upper Triassic of Australia was recognized a younger synonym of *Mesotrichopteridium*. *Necrotaulius parvulus* and *Mesotrichopteridium intermedium* are the only representatives of Necrotauliidae in the Lower Toarcian of Europe and regarded as stem group members of *Amphiesmenoptera. The ovipositor, like terminalia of female *N. parvulus* (Fig. 1A), indicate that these insects laid their eggs rather in soil than in water.

Liadotaulius maior (HANDLIRSCH, 1906) (Fig. 1D-G, 2H-K) is the oldest known genuine trichopteran with a plesiomorphic set of venational characters in the female which hinders a familiar placement. The male wings of *Liadotaulius*, comparable to *Oncovena* NOVOKSHONOV & SUKACHEVA, 1995, have an autapomorphic corema built of the distal fusion of R_1 and R_2 which was suitable as a scent container (Fig. 1E). Basal trichopteran forewings can be recognized as such by the bend of the apical part of CuP towards the wing margin and its desclerotisation. The value of this character, fixed by KRISTENSEN (1997), can now be verified in the early fossil record of the Trichoptera.

The following monotypic genera described within Necrotauliidae belong to the Lepidoptera (ANSORGE, 2002): *Pseudorthophlebia* HANDLIRSCH, 1906, *Nannotrichopteron* HANDLIRSCH, 1906, *Pararchitaulius* HANDLIRSCH, 1939, *Parataulius* HANDLIRSCH, 1939 and *Archiptilia* HANDLIRSCH, 1939. They can be recognized as such by the presence of scales on the wing surface and three medial veins in the forewing.

Hindwings of *Paratrichopteridium* HANDLIRSCH, 1906 belong either to *Liadotaulius* or Lepidoptera.

The systematic position of *Trichopteridium gracile* GEINITZ 1880, *Necrotaulius affinis* HANDLIRSCH 1939 (= *Necrotaulius handlirschi* FISCHER 1962), *Necrotaulius vicinus* HANDLIRSCH 1939, *Necrotaulius regularis* HANDLIRSCH 1939 and *Liadoptilia misera* HANDLIRSCH 1939 remains obscure.

III. DISTRIBUTION OF AMPHIESMENOPTERA IN THE LOWER TOARCIAN OF GERMANY

The insects which were buried in the marine Lower Toarcian taphocoenoses had lived on various mainlands surrounding the epicontinental sea (ANSORGE 2003). The insects from Grimmen and Dobbertin had lived on the Fennoscandinavian mainland or on offshore island in the North, the source of the Bavarian (Mistelgau, Kerkhofen) and Suevian (Holzmaden) insects is to be searched on the Bohemian Mass and/or the Vindelician Land in the south. The insects from the Braunschweig area come either from the Hercynian-Bohemian or Rhenic Masses.

The distribution of amphiesmenopterans in various Lower Toarcian localities of Germany is the result of diagenetical and taphonomical processes, which altered the input from biocoenoses on the

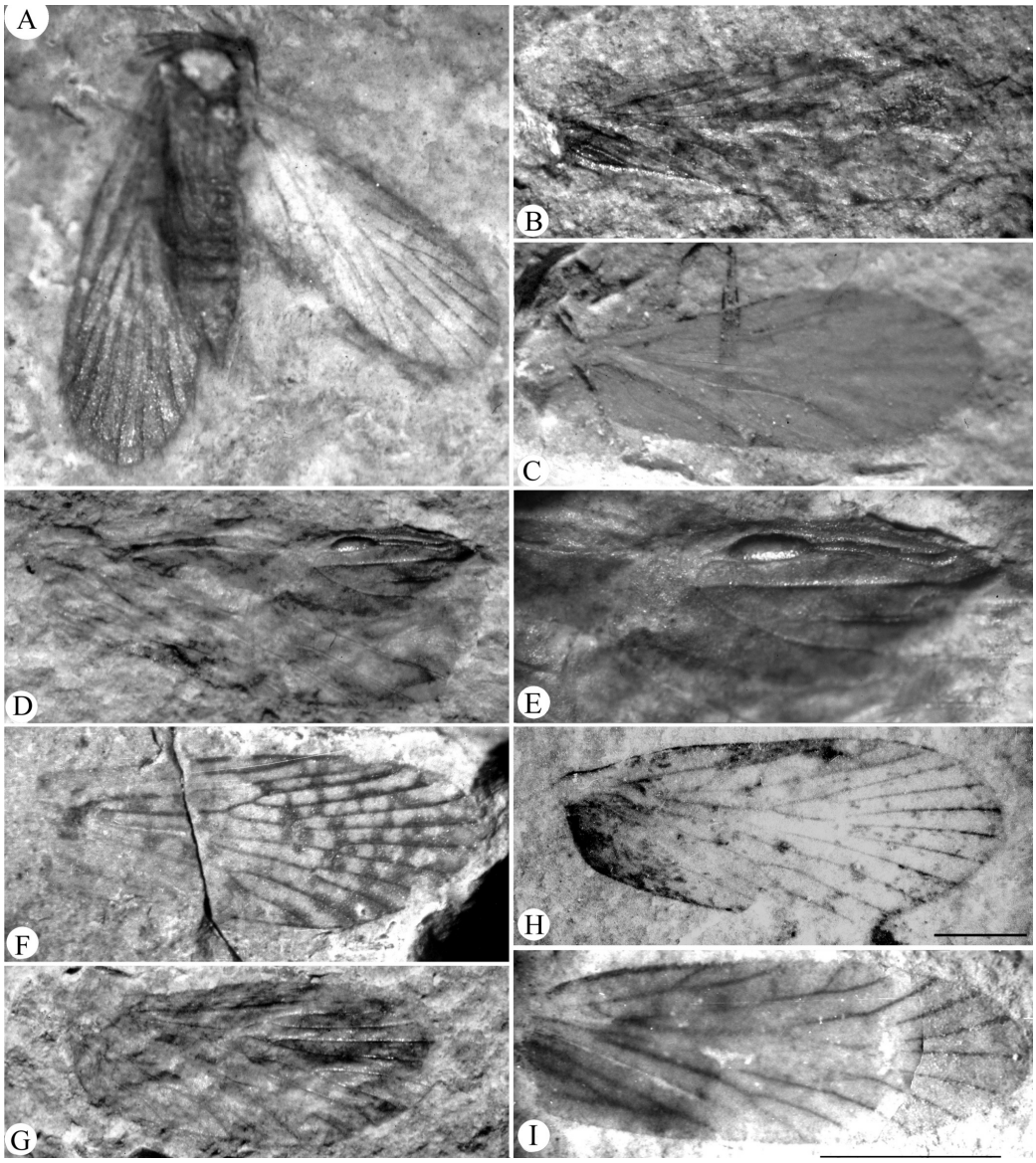

Fig. 1. Amphiesmenopterans from the Lower Toarcian of Northern Germany. A: *Necrotaulius parvulus* (GEINITZ, 1884). LGA 1097, female with fore and hindwing, Grimmen. B-C: *Mesotrichopteridium intermedium* (HANDLIRSCH, 1906). B: Holotype (FGWG 122/71), Dobbertin. C: Hindwing, LGA 784, Grimmen. D-G: *Liadotaulius maior* (HANDLIRSCH, 1906). D: male forewing, LGA 672, Grimmen. E: LGA 672, detail of the corema, built of radial veins. F: female forewing, LGA 280, Grimmen. G: Hindwing, LGA 1710 Grimmen. H: Lepidoptera, forewing, LGA 1500, Grimmen. I: Lepidoptera, forewing, LGA 2017, Grimmen. Scale 1 mm.

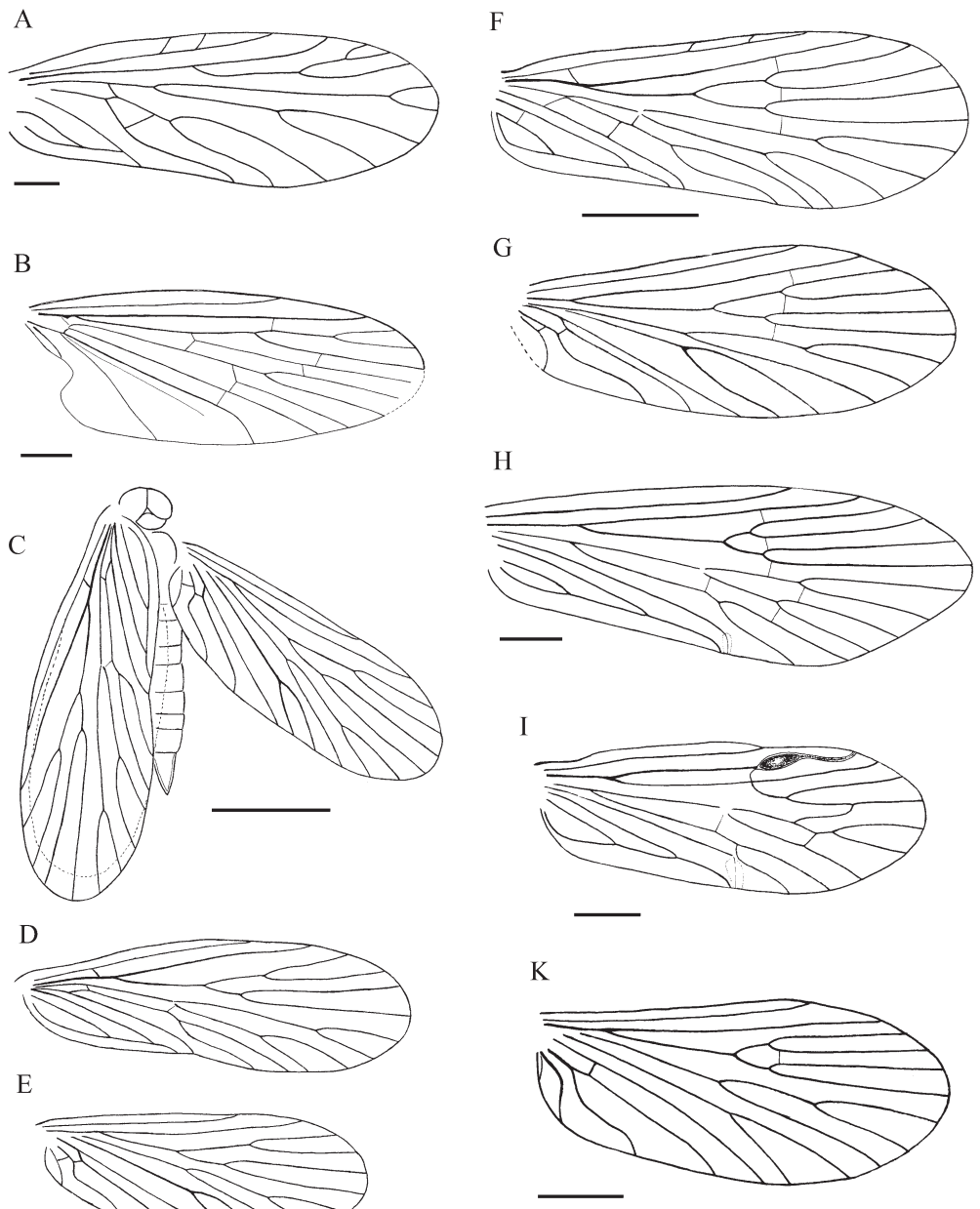

Fig. 2. Amphiesmenopterans and insects earlier described as Trichoptera from the Lower Toarcian of Northern Germany. A: *Prosepididontus calopteryx* HANDLIRSCH, 1920 (Grylloblattida: Geinitziidae), FGWG 123/88, Dobbertin. B: *Metatrichopteridium confusum* HANDLIRSCH, 1939 (Diptera: Hennigmatidae), MB.I. 44.1, Dobbertin. C-E: *Necrotaulius parvulus* (GEINITZ, 1884), LGA 1097, female with fore (D) and hindwing (E), Grimmen. F-G: *Mesotrichopteridium intermedium* (HANDLIRSCH, 1906). F: Forewing, LGA 789, Grimmen. G: Hindwing, LGA 784, Grimmen. H-K: *Liadotaulius maior* (HANDLIRSCH, 1906). H: Female forewing, LGA 1995, Grimmen. I: Male forewing, LGA 672, Grimmen. I:, Hindwing, LGA 1710 Grimmen. Scale 1 mm.

mainland. Wings with faint and not well sclerotized venation (especially lepidopterans) and most hind wings are well preserved only in Grimmen, the locality with the best preservation potential.

Necrotaulius parvulus is known from almost all Lower Toarcian insect localities in Europe. The dense pilosity of their forewings, allowing good preservation, is probably the reason for their abundance. On the other hand, *N. parvulus* undertook apparently mass migration over the sea which can explain the fair number of complete specimen in the major localities Dobbertin, Grimmen and Braunschweig. After the record of complete well preserved specimen it was possible to recognize the associated hindwings. Well preserved isolated hindwings are only known from Grimmen. At this locality one third of all *N. parvulus* findings are hindwings, 50 % are forewings.

Mesotrichopteridium intermedium, a common species in Dobbertin, was also found only in Grimmen, what can mean that it lived on the Fennoscandinavian mainland exclusively. Isolated hindwings fitting by their size to the forewings are believed to belong to *M. intermedium*.

Male and female forewings of *Liadotaulis maior* are generally rare, a few specimen are known from Grimmen and Dobbertin. Some poorly preserved wings from Braunschweig may belong to this species. Hindwings (earlier described as *Paratrichopteridium*), similar to those of *Oncovena borealis* SUKATCHEVA & NOVOKSHONOV 1995 are believed to belong to *L. maior*.

The presence of lepidopterans in the Upper Liassic of Grimmen (NE-Germany) was first recorded by ANSORGE (1996). This was the second record of Liassic lepidopterans. Older is only the poorly preserved *Archaeolepis mane* WHALLEY 1985 from the Sinemurian of Dorset (England). Lepidopterans, which are still not studied in detail, are rather common in Grimmen and Dobbertin, present in Lower Saxony but poorly preserved there. The fair number of lepidopterans in Grimmen and Dobbertin may indicate that these species, like *Necrotaulius parvulus*, undertook active dispersion flights as it is also known from the Lower Tertiary Fur Formation of Denmark (RUST 2000) On the basis of abundant and well preserved material from Grimmen it is possible to distinguish at least two well discernible species of Lepidoptera related to Micropterygidae (Fig. 1 H-I). The determination of the new material, however, is hindered by the poor preservation of the lepidopteran type material.

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Appendix

***Necrotaulius parvulus* (GEINITZ, 1884)**

= *Necrotaulius marginatus* (BODE, 1905) [Brunswick]

= *Necrotaulius dobbertinensis* HANDLIRSCH, 1906 [Dobbertin]

= *Necrotaulius nanus* HANDLIRSCH, 1906 [Dobbertin]

= *Necrotaulius pygmaeus* TILLYARD, 1933 [England]

= *Necrotaulius bodei* HANDLIRSCH, 1939 [Brunswick]

= *Necrotaulius minimus* HANDLIRSCH, 1939 [Dobbertin]

= *Necrotaulius pygmaeus* HANDLIRSCH, 1939 [subst. by FISCHER 1962] [Dobbertin]

= *Necrotaulius obtusior* BODE, 1953 [Brunswick]

***Mesotrichopteridium intermedium* (HANDLIRSCH, 1906)**

= *Necrotaulius similis* HANDLIRSCH, 1906 [Dobbertin]

= *Mesotrichopteridium pusillum* HANDLIRSCH, 1906 [Dobbertin]

= *Necrotaulius maculatus* HANDLIRSCH, 1920 [Dobbertin]

= *Necrotaulius pullus* HANDLIRSCH, 1939 [Dobbertin]

= *Necrotaulius megapolitanus* HANDLIRSCH, 1939 [Dobbertin]

= *Necrotaulius ellipticus* HANDLIRSCH, 1939 [Dobbertin]