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RESEARCH PAPER

New fossil insects from the Anisian (Lower to Middle Muschelkalk) from the Central European Basin (Germany and The Netherlands)

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Abstract The Palaeozoic–Mesozoic transition is characterized not only by the most massive Phanerozoic mass extinction at the end of the Permian period, but also its extensive aftermath and a prolonged period of major biotal recovery during the succeeding Middle to Late Triassic. Particularly, Anisian insect species from units of the Lower to Middle Muschelkalk from the Central European Basin are rare. The specimens described here originated from the Anisian Wellenkalk facies (Lower Muschelkalk), Vossenveld Formation of the Winterswijk quarry, The Netherlands, and from the *orbicularis* Member (lowermost Middle Muschelkalk, Anisian) of Esperstedt near Querfurt (Saxony-Anhalt). Thus, the described insect remains from Winterwijk and Esperstedt expand our knowledge about Middle Triassic terrestrial arthropod communities and their palaeodiversity. A new species of *Chauliodites* (*C. esperstedti* sp. nov) is introduced.

Keywords Middle Triassic · Anisian · Muschelkalk · Vossenveld Formation · Insects · Winterwijk · Esperstedt

Kurzfassung Der Übergang vom Paläozoikum zum Mesozoikum ist nicht nur durch eines der größten Massenaussterben des gesamten Phanerozoikums charakterisiert, sondern ist auch gekennzeichnet durch eines der zeitlich längsten Erholungsmuster terrestrischer Ökosysteme – vermutlich erst einsetzend während der mittleren bis späten Trias. Fundstellen für mitteltriassische Insekten, insbesondere aus Einheiten des unteren bis mittleren Muschelkalk, sind in Mitteleuropa gewöhnlich sehr selten. Die hier untersuchten Proben stammen vornehmlich von der Fundstelle Winterswijk, Niederlande (Vossenveld-Formation, Wellenkalk Fazies, Unterer Muschelkalk), wobei aus den '*Orbicularisschichten*' (unterster Mittlerer Muschelkalk) von Esperstedt, nahe Querfurt (Sachsen-Anhalt), nur ein isolierter Fund beschrieben wird. Somit kommt den Fundstellen Winterwijk und Esperstedt eine besondere Bedeutung zu, weil sie hinsichtlich ihres gut erhaltenen und diversen Fossilinhalts bedeutende Fundorte für mitteltriassische Insektenreste darstellen und uns einen Einblick in die Ökologie und Ausbildung terrestrischer Lebensräume der mittleren Trias gewähren. Eine neue Art der Gattung *Chauliodites* (*C. esperstedti* sp. nov.) wird beschrieben.

Schlüsselwörter Mittel Trias · Anisium · Muschelkalk · Vossenveld-Formation · Insekten · Winterwijk · Esperstedt

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Introduction

The Mesozoic was a critical time in the evolution of insects worldwide—a period of transition from the mainly extinct assemblages of the Late Palaeozoic to a fauna having an essentially modern morphology. This changeover can be traced to the Permo-Triassic extinction event, which greatly reduced insect diversity (Clapham et al. 2016). At the current stage, only dipteran and hymenopteran clades evolved during or after the Permian/Triassic extinction event and probably even appeared before, as the stem Hymenoptera are known in the Late Carboniferous (e.g., Nel et al. 2013). In a more general view, up to 19 insect orders appeared during the entire Mesozoic time period (e.g., Misof et al. 2014; Clapham et al. 2016), which provide some vital clues to palaeoecological interpretation for former terrestrial ecosystems (e.g., Ponomarenko 2016). Particularly, these orders allowed the evolved holometabolous orders, which appeared during the Late Carboniferous but remained weakly diversified in the Permian (e.g., Nel et al. 2013; Misof et al. 2014; Haug et al. 2015), to expand and diversify into now uninhabited ecospace. The change in insect fauna seems to be closely linked to the Mesozoic floral transition, beginning in the Early Triassic with the appearance of the conifers and bennettitales and culminating in the Cretaceous diversification of the angiosperms (Labandeira 2013). Nevertheless, the Early Triassic remains one of the most poorly known periods in the evolutionary history of terrestrial arthropods (e.g., Fraser et al. 1996), except for the Konservat Lagerstätte of the 'grès à Voltzia' of the Vosges, and only the end of the Triassic Period is pivotally known for the evolution of modern ecosystems (Labandeira 2005; Shcherbakov 2008a, b; Rasnitsyn et al. 2015; Ponomarenko 2016).

Herein we present the description of new Anisian insect species from units of the Lower to Middle Muschelkalk from the Central European Basin (CEB). The specimens described below originate from (1) the Anisian Wellenkalk facies (Lower Muschelkalk), Vossenveld Formation of the Winterswijk quarry, The Netherlands, which represent the first Mesozoic fossil insect remains from the Netherlands described to date; and from (2) the *orbicularis* Member (lowermost Middle Muschelkalk, Anisian) of Esperstedt near Querfurt (Fig. 1). Thus, the newly described insect remains from the new fossil insect localities Winterwijk and Esperstedt expand our knowledge about Middle Triassic terrestrial arthropod communities and their palaeodiversity. Furthermore, the finds from Winterswijk constitute the first described insect assemblage from the Muschelkalk (Reis 1909; Müller 1967) and contribute to our understanding of the depositional setting of the outcrops at Winterswijk.

Materials and methods

The specimens RGM.792287, RGM.791779 and RGM.792411 and associated metadata are deposited at the Naturalis Biodiversity Center, Leiden, the Netherlands (RGM). The specimen AHWW-0221 is stored in the collection of Adam Haarhuis (see affiliations for contact details). The specimen NHMS–WT 2166 is stored at the Natural History Museum Schloss Bertholdsburg in Schleusingen. The described individuals were observed and digitized using a Keyence VHX-1000 microscope, and all relevant structures were measured from the digitized images.

Geological background.
Winterswijk, The Netherlands (Fig. 1a, b).

The outcrops at Winterswijk belong to the early Anisian Vossenveld Formation (Lower Muschelkalk) (Hagdorn and Simon 2010). These outcrops were deposited close to the northwestern margin of the epeiric Germanic basin and are comprised of partially laminated micritic limestones which in turn consist of alternating marly limestones, dolomites, clayey marls and dolomitic clay layers (Borkhataria et al. 2006; Klein et al. 2015). The strata at Winterswijk are thought to alternately document shallow marine environments and tidally influenced shabka like (hypersaline) mudflats with algal laminates, polygonal mudcracks and reptile trackways (Oosterink and Winkelhorst 2013; Klein 2012; Klein et al. 2015). For a full stratigraphic section of the Winterswijk quarry the reader is referred to Oosterink (1986). A multitude of fossils have been recovered from the Winterswijk quarry including bivalves, numerous trace fossils, reptile skeletal remains, fishes, ammonites, brachiopods, gastropods, plant remains, crustaceans, chelicerates, and possibly even scyphozoans (Herngreen et al. 2005a, b; Hauschke et al. 2009; Klompmaker and Fraaije 2011; Oosterink 2012; Oosterink and Winkelhorst 2013; Maxwell et al. 2016). Additionally, a single insect wing from Winterswijk has previously been informally described by Oosterink, first as a roachoid (Oosterink 1987) and later re-interpreted as a dragonfly (Oosterink 2012). This wing might even correspond to the posterior part of the cubito-median area of a Triadophlebiomorpha, based on the photograph displayed in Oosterink (1987). Unfortunately, this wing was not available for re-examination. However, by re-examining the available literature it was possible to determine that this wing most likely originated from layer 33 (numbering according to Oosterink 1986) and can thus be palynologically dated to the Bithynian substage of the Anisian (Oosterink 1986, 1987; Herngreen et al. 2005a, b). The stratigraphic context of the insect remains discussed in this publication is also well known. The specimen

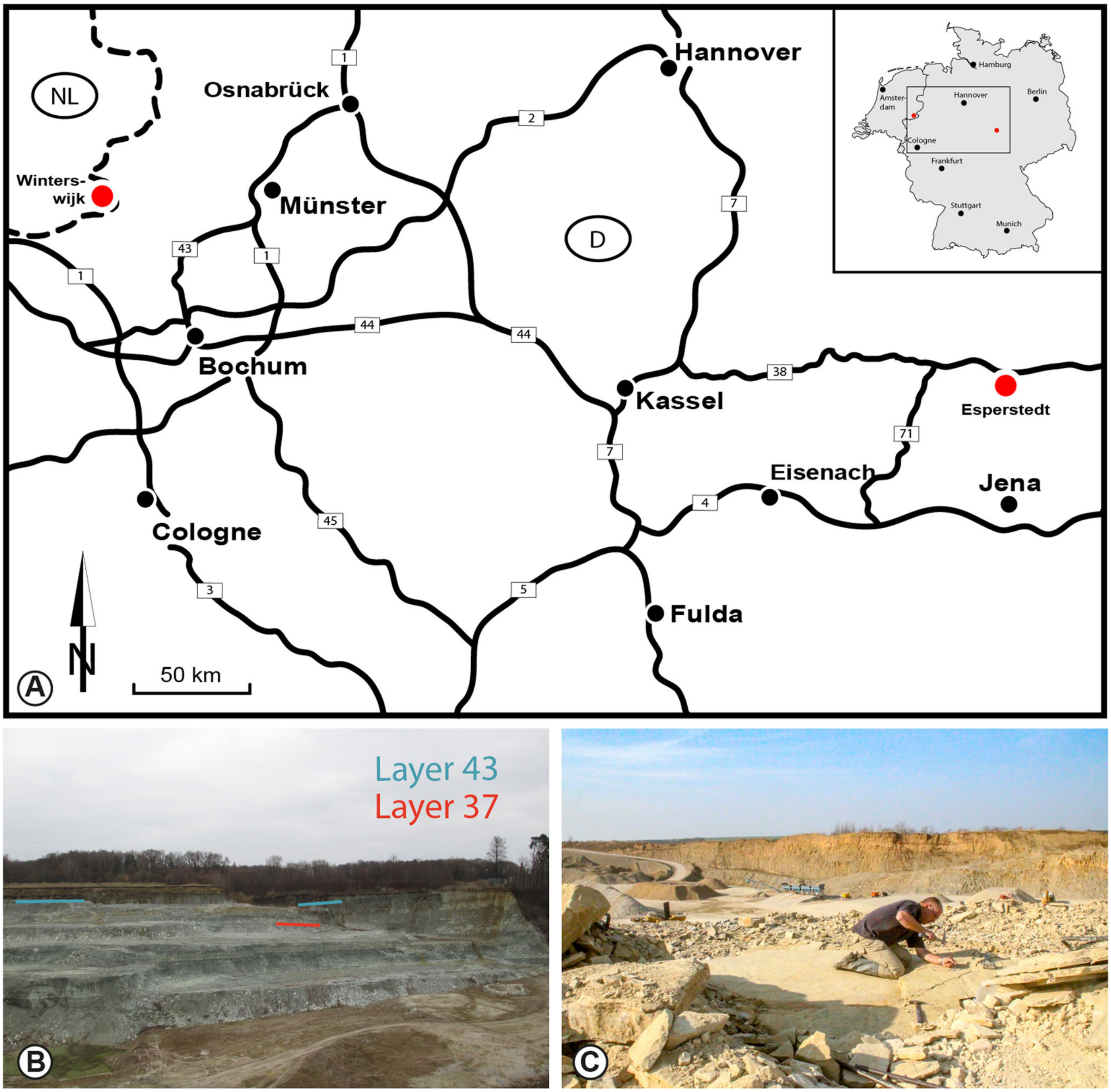
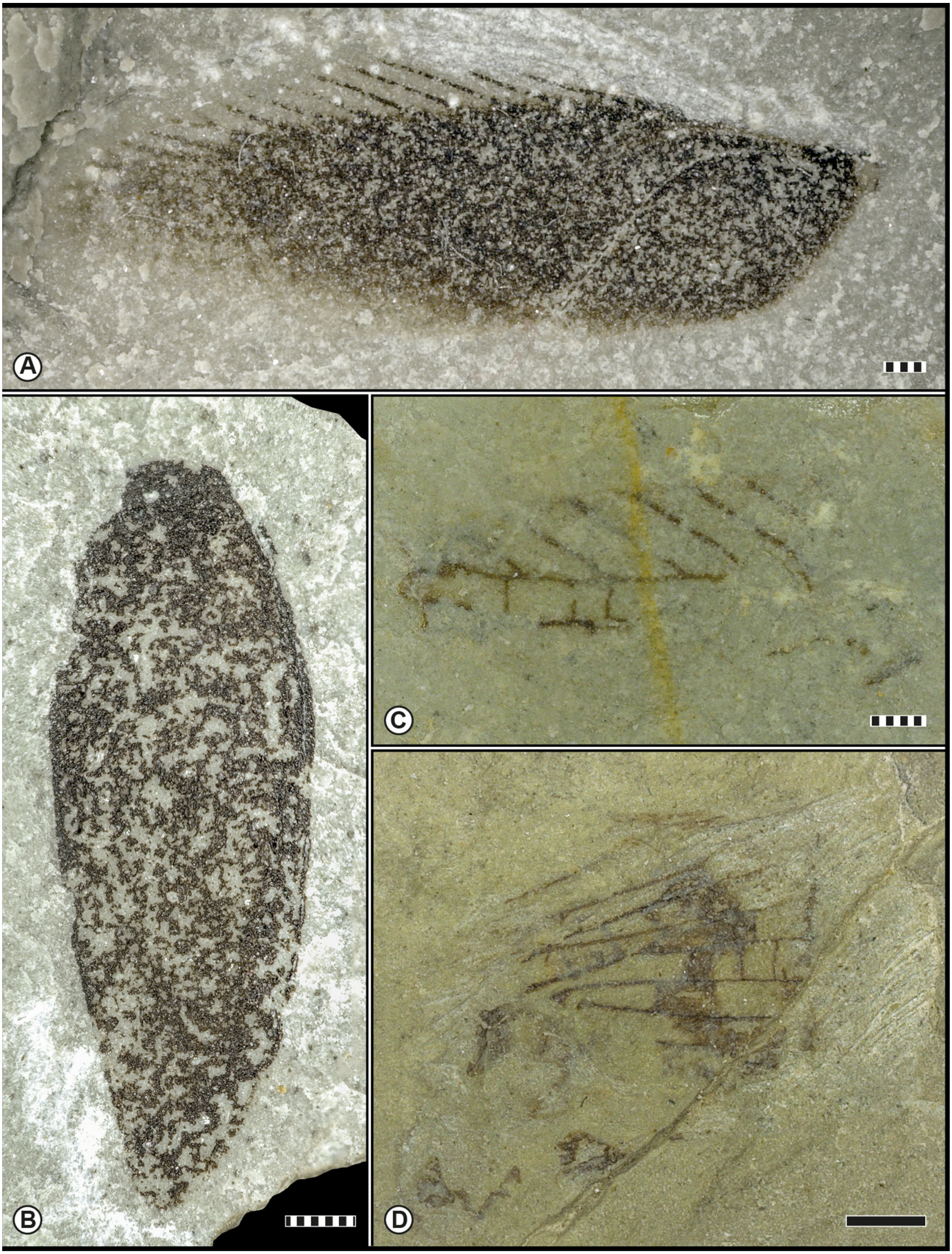


Fig. 1 **a** Map showing the fossil localities of Winterswijk (Netherlands) and Esperstedt near Querfurt (Saxony-Anhalt, Germany). **b** The Winterswijk quarry with the layers 37 and 43 marked in *red* and *blue*, respectively (image courtesy of Gerard Goris). **c** Esperstedt quarry during a visit in 2012 (image courtesy of Jos Lankamp)

RGM.792287 (Fig. 2a) was found in layer 37 (Oosterink 1986). Using the palynological evidence presented by Herngreen et al. (2005a, b) it is possible to assign a Bithynian age to this layer. The specimens AHWW-0221 (Fig. 2b), RGM.791779 (Fig. 2c) and RGM.792411 (Fig. 2b–d) originate from layer 43, a layer of the Winterswijk quarry that has only recently been exposed. Layer 43 is considered to be Illyrian in age (Hagdorn and Simon 2010; Maxwell et al. 2016). Although this Illyrian date for layer 43 is upheld in this publication, it should be noted that this implies a large sedimentation gap or a severely reduced sedimentation rate between layer 37 (Bithynian) and layer 43 (Illyrian), which seems discordant with the available stratigraphic evidence. Novel stratigraphic investigations concerning the age of layer 43 therefore seem paramount. Both layer 43 and layer 37 are known to have yielded plant remains (Goris, pers. observation 2016; Reumer, pers. observation 2016).


A
B
C
D

◀**Fig. 2** Insects from the Anisian (Lower to Middle Muschelkalk) from the Central European Basin (CEB). **a–d** Incompletely preserved wings, elytra and tegmen from the Vossenveld Formation, early Anisian (Lower Muschelkalk) of Winterswijk (Netherlands). **a** Undetermined cockroach tegmen. **b** Isolated elytra. **c** Undetermined insect wing fragment. **d** Undetermined insect wing fragment. *Scale bars striped* 0.5 mm, *solid* 1 mm

Esperstedt, Saxony-Anhalt, Germany (Fig. 1a, c).

The *orbicularis* Member (lowermost Middle Muschelkalk) consists of yellow silty platy dolomites, laminated mud-cracked black marls/yellow dolomites, yellow dolomites, laminated mud-cracked carbonatic marls, bioturbated yellowish mud-cracked dolomitic marls, and grey-green silty marls. In the basal area of this member the index fossil *Neoschiozodus orbicularis* ('Orbicularisschichten') occurs together with a few other, mostly poorly preserved molluscs. Locally, the dolomite contains abundant vertebrate remains (fish remains, saurian bones and teeth). H. v. Meyer (1851) described a rich fauna of this level from Esperstedt near Querfurt (see also Rieppel and Wild 1996).

Systematic palaeontology

Superorder **Blattodea** Brunner van Wattenwyl, 1882
Family undetermined
Figure 2a

Studied material. Specimen RGM.792287, strongly sclerozized tegmen.

Description. A tegmen strongly sclerotized, with only the costal branches of subcostal of radius still individualized, all simple and parallel, except for two or three in the costo-apical part of wing, no other vein visible in the rest of the tegmen, except for the anterior limit of anal area basally straight, with a pronounced curve in its basal third and distally straight; tegmen 9.4 mm long, 3.3 mm wide; anal area 1.9 mm wide, 4.0 mm long.

Remarks. The classification of modern cockroaches has long been contentious, and many classifications have been proposed and debated, each using a different morphological feature as the main focus. Venation, which is the main feature used in the classification of most other insect orders, was considered inappropriate for the taxonomy of the modern cockroaches. Nevertheless, Martins-Neto et al. (2005) used the relative positions of the primary M fork (their 'oMA'), length of clavus ('amL') and length of costal region ('l cm') to define the family status of Late Triassic Argentinean 'blattodeans', but this arrangement could not be considered for the taxonomy of the Winterwijk material, as the tegmen is too strongly sclerotized. Unfortunately, without more completely preserved wings and other associated material, it is difficult to be more specific in their identifications.

Stratigraphic and geographic distribution. Winterswijk, The Netherlands. Vossenveld Formation, Layer 37, Bythinian, earliest late Anisian (Lower Muschelkalk).

Order **Coleoptera** Linnaeus, 1758
Family undetermined
Figure 2b

Studied material. Specimen AHWW-0221; single isolated elytra.

Description. A single elytron, 5.5 mm long, 1.9 mm wide; with apex acute, shoulder not pronounced, outer margin regularly arched; surface covered with small punctuations not aligned; no trace of veins or furrows visible.

Remarks. This isolated elytron is impossible to place in a precise beetle lineage. It shows strong similarities with the 'species 25' or 'species 26', figured in Papier et al. (2005): (Fig. 6 A-B) from the Early Anisian of the Vosges (France). To our knowledge this is the oldest known coleopteran fossil from the Netherlands.

Stratigraphic and geographic distribution. Winterswijk, The Netherlands. Vossenveld Formation, Layer 43, Illyrian, earliest late Anisian (Lower Muschelkalk).

Order undetermined
Figure 2c

Studied material. Specimen RGM.791779.

Remarks. Specimen RGM.791779 is a further wing fragment of insect, ca. 4 mm long, showing the apical part of SC, emitting at least seven parallel anterior veinlets in costal area, fragments of radial vein and three crossveins between R and SC. The rather wide area between R and SC would exclude affinities with the Neuroptera. This pattern of venation can be observed in some Orthoptera. But it is impossible to be more precise regarding the affinities of this fossil.

Stratigraphic and geographic distribution. Winterswijk, The Netherlands. Vossenveld Formation, Layer 43, Illyrian, earliest late Anisian (Lower Muschelkalk).

Order undetermined ('Grylloblattida?')
Figure 2d

Studied material. Specimen RGM.792411; incomplete weing fragment.

Remarks. An incomplete mid part of a grylloblattid forewing, which probably belongs to Chauliodititidae based on the preserved parts (vide infra). RS and MA simple. Crossveins are simple and form double or triple rows of cells. Color pattern and venation seem to be similar to that of *Chauliodites* *esperstedtensis* sp. nov. Due to this resemblance, the wing may belong to the new species described from Esperstedt. Considering its poor preservation, however, it seems more prudent to consider the material undeterminate.

Stratigraphic and geographic distribution. Winterswijk, The Netherlands. Vossenveld Formation, Layer 43, Illyrian, earliest late Anisian (Lower Muschelkalk).

Order '**Grylloblattida**' Walker, 1914 (sensu Storozhenko 2002)

Family **Chauliodititidae** Handlirsch, 1908
Genus ***Chauliodites*** Heer, 1864

Type species. *Chauliodites picteti* Heer, 1864 by original designation.

Chauliodites esperstedtensis sp. nov.
Figure 3a, b

Etymology. Named after the type locality Esperstedt.
Holotype. NHMS–WT 2166, isolated forewing, stored at the Natural History Museum Schloss Bertholdsburg in Schleusingen.

Locality and horizon. Esperstedt near Querfurt (Saxony-Anhalt), Germany. Part of the *orbicularis* Member (lowermost Middle Muschelkalk).

Diagnosis. Forewing characters only. Two dark bands in distal part of wing; fork of CuA basal of base of RS; forks of RS, MP, and MA at the same level; MA simply forked; MP forked; no double row of cells in radial area; SC not reaching apical quarter of wing; SC straight at its base.

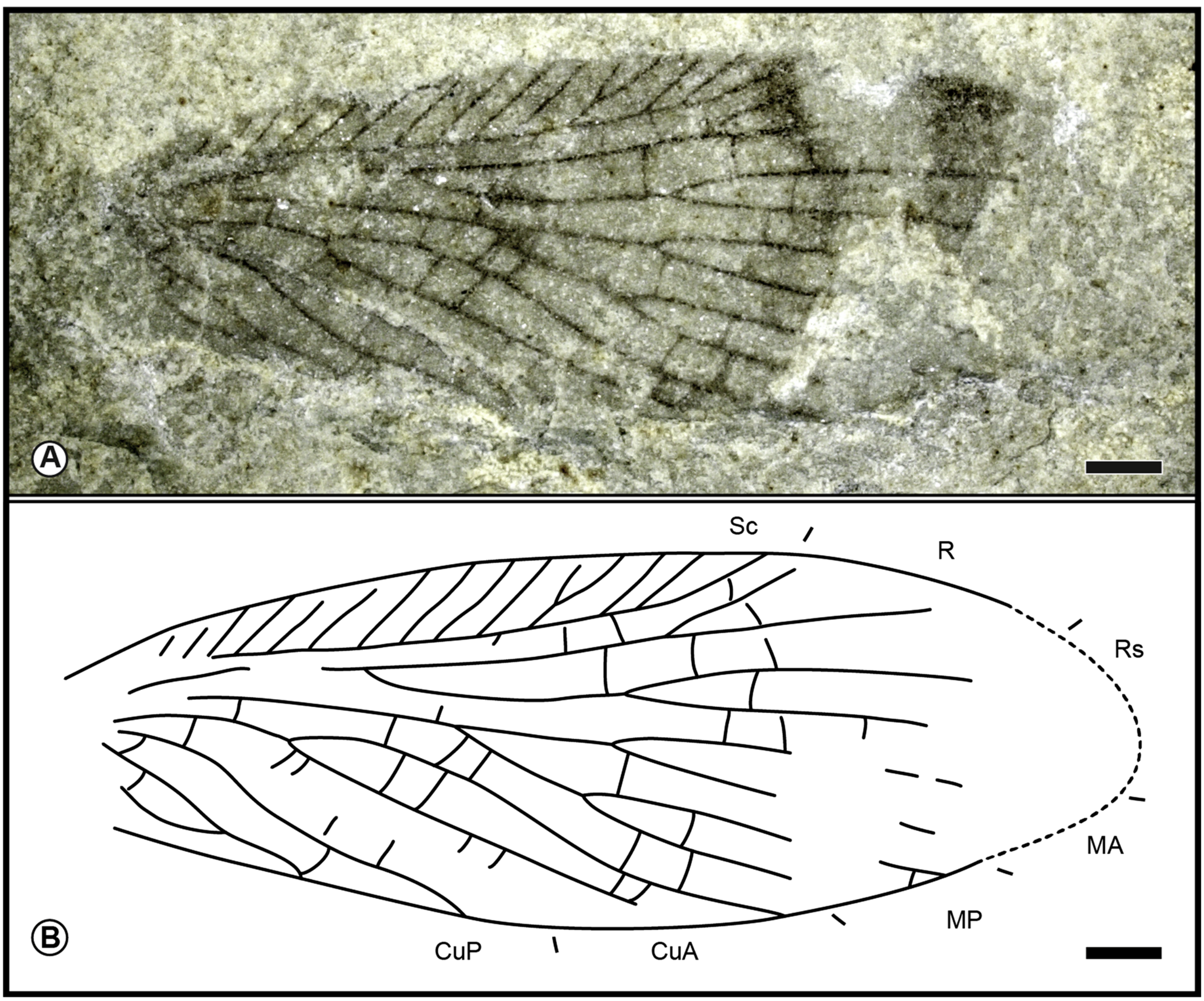


Fig. 3 Insects from the Anisian (Lower to Middle Muschelkalk) from the Central European Basin (CEB). **a, b** Isolated forewing from the *orbicularis* Member (lowermost Middle Muschelkalk) from Esperstedt near Querfurt (Saxony-Anhalt), Germany. **a** *Chauliodites esperstedtensis* sp. nov., photograph. **b** *Chauliodites esperstedtensis* sp. nov., drawing. *Scale bar solid* 1 mm

Description. Forewing length ca. 12.0 mm, width 4.8 mm, hyaline except for two transverse darker zones in distal half of wing and two small dark spots near base of RP and fork of M, wing covered with microtrichiae; several strong cross-veins situated in radial, median, cubital and anal areas; ca. 15 strong cross-veins in costal area, all simple except one forked; SC long, ending on costal margin 9.2 mm from wing base; base of RS 4.0 mm from wing base; RS with two branches, forked 3.4 mm from its base; R forked near its apex; fork of M into MA and MP distinctly distal (3.2 mm) of base of RS, both MA and MP distally forked; an oblique convex arculus ('M5') between median stem and CuA; CuA divided into CuA1 and CuA2 slightly basal (1.2 mm) of level of base of RS; both CuA1 and CuA2 simple, sigmoidally waved, with several oblique cross-veins in the area between them; three convex anal veins form together with concave simple CuP a three-celled anal loop-like structure.

Comparison. *Chauliodites esperstedtensis* sp. nov. has its vein CuA with only two simple branches (especially CuA1 simple). This character is really infrequent among the Grylloblattida, in which a majority of taxa has a least a three-branched CuA (see Storozhenko 1998). *C. esperstedtensis* has a forewing venation nearly identical to that of the Triassic *Chauliodites picteti* Heer, 1864 (Germany), even in the distribution of the dark spots (Bashkuev et al. 2012). Aristov et al. (2009a: 282) proposed the following diagnosis for the Chauliodititidae Handlirsch (1906): 'Costal space broader than subcostal one; M not fused with CuA, branching beyond RS base; CuA divided into CuA1 and CuA2'. *C. esperstedtensis* has all these characters.

Nevertheless, *C. esperstedtensis* also has a very particular character present in the Jurassic geinitziid genera *Sinosepididontus* Huang and Nel, 2008 and *Prosepididontus* Handlirsch, 1920, i.e., a celled anal loop (Huang and Nel 2008). But, after the key to geinitziid genera of Cui et al. (2012: 259), *C. esperstedtensis* does not correspond to any of the genera, because it would fit with the two genera *Sinosepididontus* and *Prosepididontus* for the presence of an anal loop structure while it has a vein R apically forked, unlike in these genera (Ansorge and Rasnitsyn 2000). The Geinitziidae also have the fork of M not so distal relatively to the base of RS *C. esperstedtensis* and the Chauliodititidae.

The anal area is very frequently lost, or not well preserved in the various chaulioditid specimens. Nevertheless, *Chauliodites cancellata* Aristov, 2003, shows an anal area with the same pattern of loops as in *C. esperstedtensis* (see Aristov 2003: Fig. 1b).

They are dominant and most common in Early Triassic insect assemblages (Ansorge and Brauckmann 2008; Shcherbakov 2008a, b; Aristov et al. 2009b; Bashkuev et al. 2012).

Within this family, *C. esperstedtensis* differs from *Permyak* Aristov (in Aristov et al. 2013a) in RS without any branch reaching anterior wing margin. It differs from *Purtovinia* Aristov (in Aristov et al. 2013b), *Triadosialis* Handlirsch, 1906, *Iphikozulu* Aristov and Mostovski, 2009, *Protomia* Aristov, 2004a, and *Miralomia* Aristov, 2004a in CuA1 simple (Aristov 2004a, b; Aristov and Bashkuev 2008; Aristov and Mostovski 2009; Aristov et al. 2009a). We can note that these genera do not share one of the main characters of the family, i.e. a simple CuA1. Furthermore, the new species differs from *Paratomia* Aristov, 2003 in the M forked into MA and MP, each of them also being simply forked (Aristov 2003). *Nivopteria* Lin, 1978 is based on a very incomplete forewing, difficult to compare to the other Chauliodititidae (Lin 1978). Aristov (2003) indicated that its costal area is four times as wide as subcostal area, which is not the case for *C. esperstedtensis*. The wing venation of *C. esperstedtensis* fits quite well with that of *Chauliodites* Heer, 1864.

Remarks. *C. esperstedtensis* is longer than that of *Chauliodites kitshmengensis* Aristov, 2013 (12 mm versus 9 mm), which also has only a dark spot at the level of branches of RS, instead of a band (Aristov 2013). In *C. nedubrovensis* Aristov, 2013, the fork of CuA is opposite the base of RS and fork of MA is distinctly basal of that of MP. *C. niedzwiedzkii* Aristov et al., 2013b and *C. issadensis* Aristov, 2009 have a MP simple (Aristov 2009; Aristov et al. 2013b). *C. durus* (Aristov, 2003), *C. cancellata* (Aristov, 2003), *C. antiqua* (Aristov, 2003), *C. ramosa* (Aristov, 2003), *C. fuyuanensis* Lin, 1978, *C. afonini* Aristov, 2008, *C. gomankovi* Aristov, 2008, *C. ponomarenkoi* Aristov, 2008, *C. circumornatus* Aristov et al., 2013b, and *C. costalis* (Martynov, 1936) have a double row of cells in the radial area (Aristov 2003; 2008; Aristov et al. 2013b). *C. sennikovi* (Aristov, 2003) has first fork of MA well basal of that of MP. *C. mongolicus* Aristov, 2005 has a five-branched MA (Aristov 2005). *C. issadensis* Aristov, 2009 has a longer SC (Aristov 2009). *C. anisicus* Aristov et al., 2011 has a sharp bent of SC at the base, unlike *C. esperstedtensis* (Aristov et al. 2011). *C. picteti* Heer, 1864 differs in the presence of dark spots instead of two dark bands in distal half of the wing (Bashkuev et al. 2012; Ansorge and Brauckmann 2008). Also its fork of MA is not aligned with those of RS and MP, unlike in *C. esperstedtensis*.

Discussion

The most complete entomofaunal successions of the Late Permian and Early Triassic (across the Permian–Triassic boundary) have been found in European Russia (Shcherbakov 2008a, b). However, on a global scale insects are rarely recorded from the Early to early Middle Triassic, and findings are mainly restricted to freshwater deposits of lakes and floodplains, particularly in the Central European Basin (CEB) (e.g., Żyła et al. 2013; Kustatscher et al. 2014). Brauckmann and Schlüter (1993) mentioned 17 specimens from the Upper Buntsandstein (uppermost Röt, Early Anisian) of Hammelburg (Lower Franconia, Bavaria), while at the same time along the western edge of the CEB deltaic deposits are dominant, forming the most significant Central European Triassic deposit also known as Grès à Voltzia from the early Middle Triassic (Early Anisian) of the Vosges mountains in France (e.g., Gall and Grauvogel-Stamm 2005; Papier and Grauvogel-Stamm 1995; Gall 1996). Marine influences in the CEB could be recognized from parts of the Middle and, particularly, the Upper Buntsandstein, in which the clastics and carbonates of the latter gradually pass upwards into the marine Muschelkalk limestones. Insect remains of the Muschelkalk age are generally rare and badly preserved and have been studied on only two occasions. The Bavarian geologist Otto M. Reis was the first to describe an approximately 6.5 cm long central portion of an insect wing (Triadotypomorpha) showing a complex wing venation from Münnerstadt, Franconia (Lower Muschelkalk, Anisian) (Reis 1909; Nel et al. 2001). The other known specimen was described by Müller 1967. He reported a complete elytron from a small beetle ('*Elytron*' *oligostriatum*) originated from the upper units of the Upper Muschelkalk ('Ceratitenschichten') (Ladinian), which had been drilled from a depth of 1446 m in KB Flieth 1/64 (Uckermark, NE-Brandenburg, Germany; Müller 1967). This makes the Winterswijk quarry the only Muschelkalk locality from which multiple insect fossils are described. Furthermore, disarticulated insect remains have now been described from three distinct layers in the top part of the Winterswijk quarry. Additionally, some of these layers in the upper section of the Winterswijk quarry have also yielded plant remains (layers 37 and 43) and palynomorphs (layer 33–38; Herngreen et al. 2005a). These pollen, spores, plant fossils, and insect fossils clearly illustrate more terrestrial influence in the upper section (layer 29 and upwards, see Oosterink 1986) and specifically in the layers 37 and 43 of the Muschelkalk in Winterswijk. It should also be noted that the excellent preservational state of the grylloblattid wing from Esperstedt certainly warrants further exploration of the strata in the Esperstedt quarry. In addition, the two new fossil insect localities described here may illustrate that the paucity of information on fossil insects from the Lower to Upper Muschelkalk appears to be due more to a lack of suitable sediments and localities rather than a lack of exploration and research. Thus both new fossil insect localities from which finds are presented here offer excellent opportunities to further explore the entomofauna of the Anisian, a crucial period in the evolutionary history of the insects.

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