



# The oldest giant lacewings (Neuroptera: Kalligrammatidae) from the Lower Jurassic of Germany

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Received 24 May 2020; received in revised form 21 June 2020; accepted 3 July 2020

Available online 9 July 2020

## Abstract

We describe the oldest Kalligrammatidae, two distantly related species of different subfamilies from the Lower Jurassic (lower Toarcian) of Germany: *Liassopsychops curvatus* Bode, 1953, *sit. nov.* (Liassopsychopinae n. subfam.) and *Ophthalmogramma klopschari* n. gen. n. sp. (Kallihemerobiinae). They lived in warm and relatively dry conditions. Subfamily Liassopsychopinae includes the Jurassic genera *Liassopsychops* and *Huiyingogramma*, *sit. nov.*, which bear forewings characterized by Sc and RA not fused distally; MP, CuA, CuP, and A1 dichotomously branched; and a well-developed central eye-spot. The forewing of *Ophthalmogramma* n. gen. is most similar to that of *Apochrysogramma* Yang et al., 2011. The diversity of early Toarcian kalligrammatids indicates a late Triassic–earliest Jurassic origin of the family. A modified classification of the central eye-spots is proposed based on the presence/absence of four main components, i.e., the central pigmented disc (A), swellings (B), oculus (C), and outer rings (D). The function of the swellings is unclear, but they may have served as pheromone containers. © 2020 Elsevier B.V. and Nanjing Institute of Geology and Palaeontology, CAS. All rights reserved.

**Keywords:** Lower Jurassic; Toarcian; Kalligrammatidae; Liassopsychopinae; Kallihemerobiinae

## 1. Introduction

The Mesozoic Kalligrammatidae are the most attractive insects in the order Neuroptera. The family contains the largest species within the order, with forewings up to 160 mm long (Bechly and Makarkin, 2016). Most are characterized by conspicuous eye-spots on the fore- and hind wings, and mouthparts with a long proboscis, by which they superficially resemble tropical butterflies (Labandeira et al., 2016).

The first species of Kalligrammatidae was described by Walther (1904) from the famous Upper Jurassic (Tithonian) Solnhofen Lithographic Limestone, i.e., *Kalligramma haeckeli*. Handlirsch published the first reconstruction of its venation (Handlirsch, 1906, pl. 48, fig. 5) and of the complete insect (Handlirsch, 1911, pl. 10, fig. 17), often reproduced in paleontology and entomology textbooks (e.g., Abel, 1920, fig. 158; Martynova, 1962, fig. 865). Since then, knowledge of fossil kalligrammatids has considerably expanded, especially in the last two decades. The family currently comprises 49 species

belonging to 17 genera from the Middle/lowermost Upper Jurassic of China (Daohugou and Yujiagou), the Upper Jurassic of Germany (Solnhofen) and Kazakhstan (Karatau), the Lower Cretaceous of England (Tonbridge and Teffont Evias), China (Yixian Formation), Mongolia (Anda-Khuduk), Russia (Transbaikalia: Baissa), and Brazil (Crato Formation) (Handlirsch, 1906–1908, 1919; Martynova, 1947; Panfilov, 1968; Martins-Neto, 1992, 1997; Ponomarenko, 1992; Lambkin, 1994; Ren and Guo, 1996; Jarzembowski, 2001; Ren and Oswald, 2002; Ren, 2003; Zhang, 2003; Zhang and Zhang, 2003; Engel, 2005; Makarkin et al., 2009; Yang et al., 2009, 2011, 2014a, 2014b; Makarkin, 2010; Jepson et al., 2012; Liu et al., 2014, 2015; Bechly and Makarkin, 2016).

The Cretanallachiinae Makarkin, 2017 (including *Burmogramma* Liu et al., 2018) from the lowermost Cenomanian Burmese amber was considered a subfamily of Kalligrammatidae by Liu et al. (2018), primarily as each wing of *Burmogramma* bears an eye-spot like type 1 of Kalligrammatidae (see Labandeira et al., 2016) and the forewing MP (for abbreviations see “2. Material and methods”) is branched as in many Kalligrammatidae, i.e., the posterior trace of MP bears several anteriorly-directed branches. However, similar constructions

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of eye-spots and MP branching are also present in several undescribed ithonid-like species from the Jurassic of Daohugou (VM, pers. obs.). Other characters of *Burmogramma* (venation of both the fore- and hind wings, mouthparts, male and female genitalia) do not principally differ from those of other genera of Cretanallachiinae, suggesting that this subfamily is monophyletic. Their wings are characterized in particular by such symplesiomorphies at the order level as the presence of the distal nygma in both fore- and hind wings, and the long, sinuous basal crossvein between R and M in the hind wing, not detected in any Kalligrammatidae. Therefore, we cannot consider Cretanallachiinae to be members of the Kalligrammatidae based on these character states, which might be homoplasious.

The hypothesis that kalligrammatids were specialized pollinators feeding on pollen of Bennettitales and cycads was first proposed by Zherikhin (1978, 1980) and Rasnitsyn (1980) based on the mouthparts of *Meioneurites spectabilis* Engel, 2005 from the Upper Jurassic of Karatau (Kazakhstan). Since then, many long-proboscid species of Kalligrammatidae have been described. They are now generally thought to have fed on the pollen and secretions of the reproductive organs of extinct gymnosperms (mostly Bennettitales) (Labandeira, 2010; Labandeira et al., 2016).

Together with other Mesozoic long-proboscid insects (such as Mecoptera and Diptera) kalligrammatids not only reveal the high diversity of Mesozoic pollinating insects, but also highlight the diversity of Mesozoic pollinator-dependent plants prior to the dominance of angiosperms (Liu et al., 2018).

Kalligrammatidae in the Lower Jurassic was first reported by Makarkin et al. (2009) based on a photograph of specimen BSPG 2009/XIX, 11 in Tischlinger (1992) from the lower Toarcian Posidonia Shale of Kerkhofen (Oberpfalz, Bavaria). This specimen was acquired in 2009 by Bayerische Staatssammlung für Geologie und Paläontologie (Munich) as part of the private collection of Winfried Hartwig (Nuremberg) (Nose, 2010).

Another specimen of the same species was subsequently found by Michael Klopschar in the former marl pit of Schandelah near Braunschweig, who reported it as *Kalligramma* sp. (Klopschar, 2006, fig. 19.19).

These two specimens are described here as belonging to *Liassopsychops curvatus* Bode, 1953, a neuropteran species which was based on a distal wing fragment from the lower Toarcian of Grassel near Braunschweig. A second kalligrammatid species is described here, based on a fragmentary wing from the Schandelah marl pit, also made available to us by Michael Klopschar.

## 2. Material and methods

The paper is based on three specimens of Kalligrammatidae from two Lower Jurassic (lower Toarcian) localities of Germany, Schandelah and Kerkhofen (see details below in sections 3.1 and 3.2).

We follow the venational terminology of Breitkreuz et al. (2017). Terminology of wing spaces and details of venation (e.g., traces, veinlets, ORB) follows Oswald (1993).

**Venational abbreviations:** A1–A3, first to third anal veins; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; hv, humeral veinlet (i.e., basal-most subcostal veinlet); M, media; MA, media anterior; MP, media posterior; ORB, oblique radial branches; RA, anterior radius; RP, posterior radius; RP1, proximal-most branch of RP; Sc, subcosta.

**Institutional abbreviations:** BSPG, Bayerische Staatssammlung für Geologie und Paläontologie, Munich, Germany; SNHM, Naturhistorisches Museum Braunschweig, Germany; TUPCI, Institut für Geologie und Paläontologie, Technische Universität Clausthal-Zellerfeld, Germany.

## 3. Lower Toarcian localities

Fossil insects of the Lower Jurassic of middle and western Europe are abundant in a brief interval at the beginning of the lower Toarcian (ca. 182 Ma). These assemblages are unique for this time. They were deposited in black shales during the Toarcian Oceanic Anoxic Event of the European epicontinental sea (Posidonia Shale) (Jenkyns, 1988). The fossils are extraordinarily well preserved in fine-grained micritic calcareous nodules or layers formed in anoxic, calm water without bioturbation of the sediments (Ansoerge, 2003; Williams et al., 2015). Insects and marine fossils (ammonites, theuthoideans, bivalves, fishes and marine reptiles: Ansoerge, 1996; Stumpf, 2016) occur in early diagenetic limestone concretions intercalated within marine clay of the “Green Series” and Posidonia Shale, a kerogen rich oil shale in the North German Basin of the boreal epicontinental sedimentation area (Fig. 1).

Major localities are in northern (Dobbertin, Grimmen), central (vicinity of Braunschweig) and southern Germany (Franconia: Mistelgau, Oberpfalz: Kerkhofen, Swabia: Holzmaden), Switzerland, Luxembourg, Belgium, and England (Ansoerge, 2003). Insects were transported to these marine depositional settings from the surrounding mainlands (Fennoscandia, Bohemian Massif, London-Brabant Massif) and offshore islands (Fig. 1). Isolated wings dominate; rare complete specimens may be found more often in near shore localities. Aquatic larvae are completely absent, and ground dwelling arthropods are extremely rare. The insects probably mostly died during dispersal flights over the sea or were blown over it by strong seaward winds. A smaller number might have been washed in by river transport.

### 3.1. Schandelah

This locality is one of many in the vicinity of Braunschweig (Lower Saxony). Bode (1905, 1953) described numerous insects from these, mainly from the former oil shale pits of Schandelah. Other outcrops resulting from marl and oil shale mining or construction activity are situated near Hondelage, Beienrode, Flechtorf, Grassel, Hattorf and Wolfsburg (Groe Kley) (see Kopeć et al., 2018).

Detailed sections of the Posidonia Shale in this area were described by Wunnenberg (1927), Wellnhofer and Vahldiek (1986), and Klopschar (2006). According to these authors, insects are rare in the lower *elegans* nodules and common in the upper *borealis* nodules (*elegantulum* subzone) (Fig. 2).

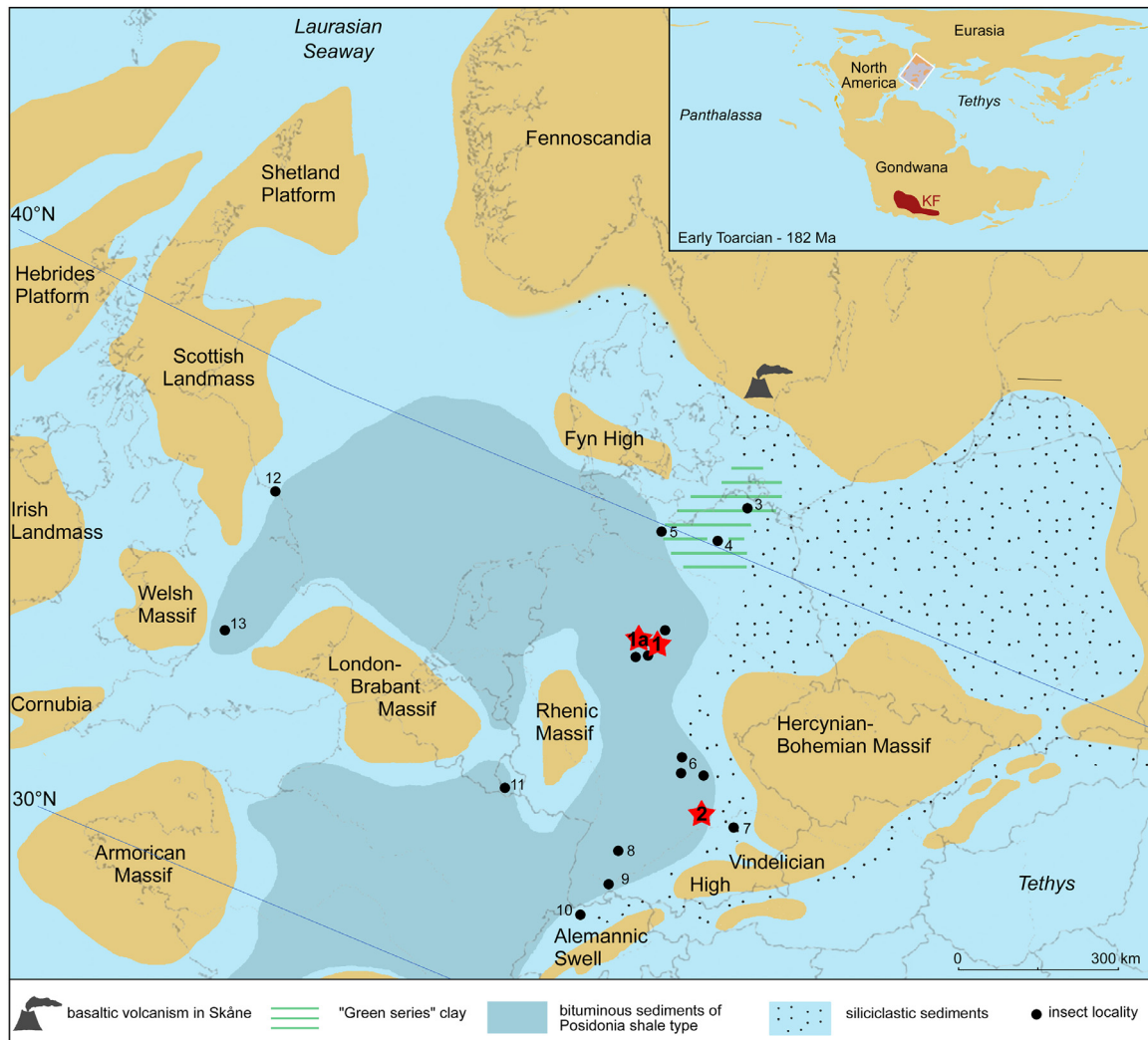


Fig. 1. Lower Toarcian paleogeography and insect localities in Middle Europe and England (red stars indicate those localities from which Kalligrammatidae are known). 1, Schandelah and Grassel (1a) in Brunswick (Braunschweig) area; 2, Kerkhofen at Rhine-Danube canal; 3, Grimmen; 4, Dobbertin; 5, Ahrensburg; 6, northern Franconia including Mistelgau; 7, Regensburg; 8, Holzmaden area; 9, Aselfingen; 10, Hemmiken; 11, Luxemburg and neighbouring Belgium; 12, Whitby; 13, Alderton and Dumbleton. Insert map shows Pangea with Karoo-Ferrar Large Igneous Province (KF) in southern Gondwana.

Both types of laminated carbonate nodules can reach 30 cm in thickness and up to 60 cm in diameter, and are lithologically similar to the so-called *siemensii* nodules or “Laibsteine” of Franconia.

Fine-grained well-laminated carbonate nodules of about 10 cm thickness with high concentrations of insects (up to 30 on rocks of 30 cm<sup>2</sup>) occur directly above a hardened marl layer, with rich gypsum and pyrite content between *elegantulum* and *borealis* nodules. We propose to name these insect nodules. Insect nodules are rare, only one (ca. 45 × 15 cm) per ca. 100 m<sup>2</sup> was observed (M. Klopschar, pers. comm.).

The kalligrammatids described below were found in *borealis* nodules from the local marl pit (Gemeindegrube) of Schandelah.

### 3.2. Kerkhofen

The Posidonia Shale was temporarily exposed for over two kilometers between the villages of Kerkhofen and Sulzkirchen

(Oberpfalz, Bavaria) during the construction of the Rhine-Danube canal in the late 1980s. Brachert (1987) described the section (Fig. 2). The Posidonia Shale of the *falciferum* zone rests unconformably (with an erosional hiatus) on blue-grey claystones of the upper Pliensbachian. One or two concretion layers of laminated, micritic limestone nodules are exposed about one meter above the base of the Posidonia Shale. These fossiliferous concretions contain abundant insects and driftwood together with marine invertebrates and vertebrates. Although these were traditionally named “*siemensii*” nodules (Krumbeck, 1932), the concretions do not yield the ammonite *Lobolytoceras siemensii* (Denckmann, 1887), an index fossil of the older *tenuicostatum* zone, but contain *Lytoceras ceratophagum* (Quenstedt, 1885) in association with ammonites characteristic of the *falciferum* zone (Riegraf et al., 1984; Riegraf, 1985).

Insects from this locality were first reported by Brachert (1987). Other insects (including the kalligrammatid

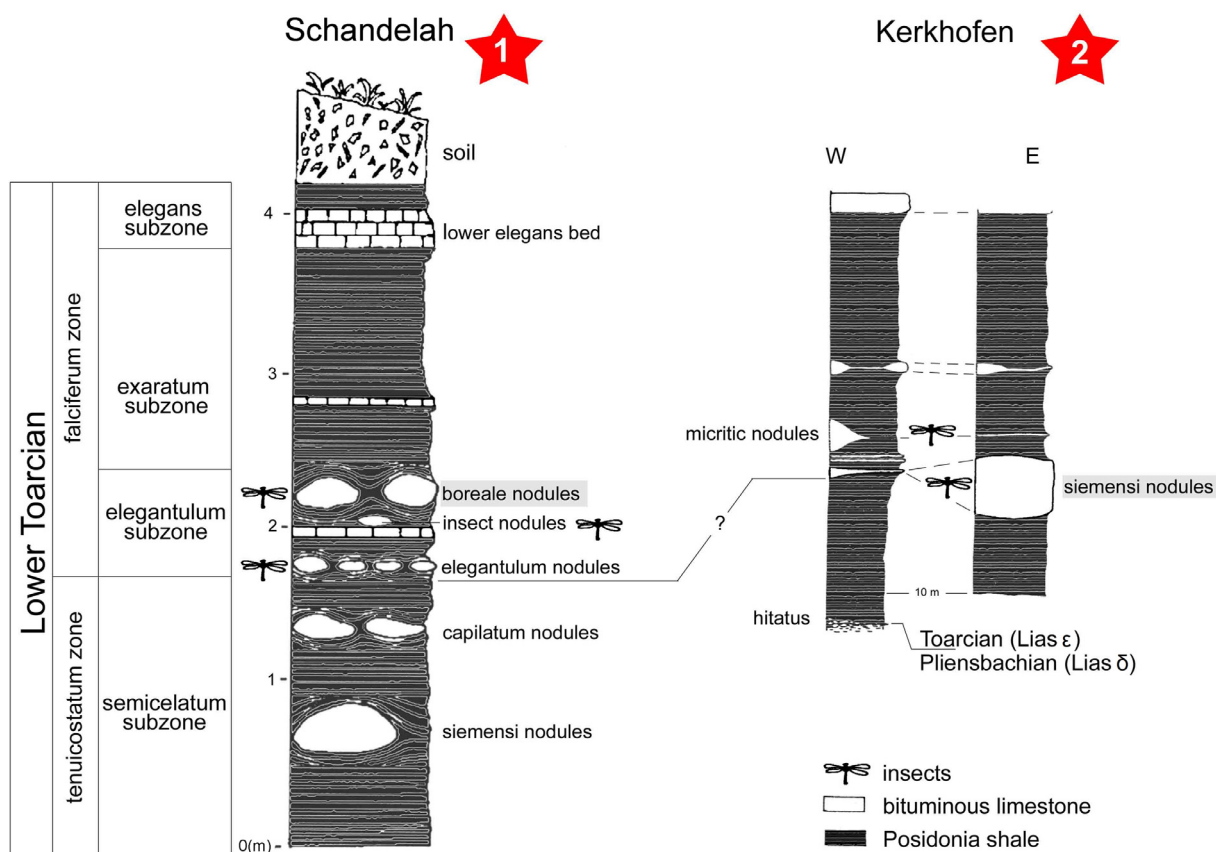


Fig. 2. Lower Toarcian Posidonia Shale sections of Schandelah and Kerkhofen, modified from Klopschar (2006) and Brachert (1987) with occurrences of insects.

described below) have been figured by Berger (1989), Tischlinger (1992, fig. 50) and Ansorge and Reich (2018), and only a few species have been described, i.e., *Liassocicada mueckeii* (Nel, 1996) (Homoptera: Tettigarctidae) and *Liassostenophlebia germanica* Fleck et al., 2003 (Odonata: Liassostenophlebiidae).

#### 4. Systematic palaeontology

Class Insecta Linnaeus, 1758

Order Neuroptera Linnaeus, 1758

Family Kalligrammatidae Handlirsch, 1906–1908 [1906]

Subfamily Liassopsychopinae n. subfam.

**Etymology:** From *Liassopsychops*, a genus-group name. The genitive case of the Greek noun *ops* is *op-os*, and its stem is *op*, and therefore the correct spelling is Liassopsychopinae (not Liassopsychopsinae).

**Diagnosis:** Forewing with recurrent, branched humeral veinlet; Sc, RA distally not fused; MP, CuA, CuP, A1 are dichotomously branched; eye-spot well developed, with two elongate swellings (sometimes indistinct, see below) within its central pigmented disc. Body, hind wings unknown.

**Genera included:** *Liassopsychops* Bode, 1953, sit. nov. (upper Lower Jurassic of Germany); *Huiyingogramma* Liu et al., 2014, sit. nov. (Middle/lowermost Upper Jurassic of China: age according to Huang et al., 2018; Upper Jurassic of Kazakhstan).

**Occurrence:** Lower Jurassic (lower Toarcian) to Upper Jurassic (Oxfordian/Kimmeridgian).

**Remarks:** Yang et al. (2014b) divided Kalligrammatidae into five subfamilies: Sophogrammatinae, Meioneurinae, Oregmatinae, Kallihemerobiinae, and Kalligrammatinae. This classification, however, is unsatisfactory. Meioneurinae are the most problematic as the three species of its single genus *Meioneurites* Handlirsch, 1906 are represented by incomplete or/and poorly preserved specimens which need re-examination. Oregmatinae and Kalligrammatinae are very similar in the venation; both have similarly-constructed long-proboscid mouthparts and similarly-constructed eye-spots (cf. e.g., *Kalligramma elegans* Yang et al., 2014a, fig. 2A and *Oregmatina illecebrosa* Yang et al., 2014b, fig. 14C). The female of *O. illecebrosa* possesses a long saber-like ovipositor like that of Dilaridae, and therefore Kalligrammatinae might also have a long ovipositor, as these subfamilies may be synonyms. The probable paraphyly of Sophogrammatinae and Kallihemerobiinae sensu Yang et al. (2014b) is discussed below.

The forewing venation of the new subfamily is most similar to that of the subfamily Sophogrammatinae. These subfamilies have the most generalized venation within the family. Yang et al. (2014b) consider the Sophogrammatinae to contain two genera, *Sophogramma* Ren and Guo, 1996 (Lower Cretaceous of the Yixian Formation, China) and *Protokalligramma* Yang et al., 2011 (Middle/lowermost Upper Jurassic of Daohugou, China). However, they are probably not closely related,

and do not form a suprageneric taxon within the Kalligrammatidae. These genera share two plesiomorphic conditions: (1) the presence of the recurrent and branched humeral veinlet (see Makarkin et al., 2013), and (2) the absence of an eye-spot. Character state (1) is clearly a symplesiomorphy at the family level, although Yang et al. (2014b, p. 26) consider this as “a synapomorphy of the subfamily”. *Protokalligramma* appears to represent the basal-most branch of the family. Its forewing venation is most similar to that of Liassopsychopinae n. subfam., sharing all diagnostic characters of the subfamily, but it notably differs by lacking the central eye-spot. This absence may be plesiomorphic in the genus, but it may be a secondary loss in *Sophogramma*. We, therefore, consider *Sophogramma* to be the only genus of Sophogrammatinae. Liassopsychopinae n. subfam. differ from Sophogrammatinae mainly by their dichotomous A1 (strongly pectinate in Sophogrammatinae) and the presence of an eye-spot.

*Sophogramma* is the single known genus of Kalligrammatidae with mandibulate mouthparts. Based on this, Yang et al. (2014b) assumed that Sophogrammatinae represent “the earliest divergence within the Kalligrammatidae” (p. 23). We believe it more likely, however, that Sophogrammatinae, Liassopsychopinae n. subfam. and *Protokalligramma* continue the main lineage leading from parakseneurid-like Neuroptera to Kalligrammatidae (see below), but unfortunately, mouthparts of the two latter taxa are unknown.

The genus *Huiyingogramma* comprises three species: *H. formosum* Liu et al., 2014 from the Middle/lowermost Upper Jurassic of Daohugou (China) and *H. turutanovae* (Martynova, 1947) from the Upper Jurassic of Karatau (Kazakhstan). A kalligrammatid forewing from Karatau reported by Ponomarenko (2002, fig. 254) as *Kalligramma turutanovae* is a new (third) species of *Huiyingogramma*. Its Sc and RA are widely separated apically (pers. obs.), but these veins in *H. formosum* are figured as fused (Liu et al., 2014, fig. 2C). However, this apparent fusion cannot be verified as it is located in a region preserved as a pale strip, the venation on which is very poorly discernible. This is also the case in *H. turutanovae*, where a possible fusion of Sc and RP is not sufficiently discernible (Martynova, 1947, fig. 2; pers. obs.). Sc and RA approach apically, but are not fused in both specimens of *Liassopsychops curvatus* (see Fig. 6).

The two genera of the subfamily may be distinguished as in the diagnosis of *Liassopsychops*.

Genus *Liassopsychops* Bode, 1953, sit. nov.

1953 *Liassopsychops* – Bode, p. 248.

**Type and only species:** *Liassopsychops curvata* [sic] Bode, 1953, by original designation.

**Emended diagnosis:** The proximal-most fork of MP located proximad the proximal-most fork of CuA (distad in *Huiyingogramma*); RP with 10–12 branches (7–9 in *Huiyingogramma*); most crossveins posterior to Sc widely spaced: distance between most crossveins longer than length of these crossveins (all these crossveins closely spaced: distance

between crossveins shorter than length of these crossveins in *Huiyingogramma*); apical eye-spot present (absent in *Huiyingogramma*).

**Occurrence:** Lower Jurassic (lower Toarcian).

**Remarks:** The genus *Liassopsychops* was previously referred to Psychopsidae (Bode, 1953; Martynova, 1962; Martins-Neto and Rodrigues, 2010) and Prohemerobiidae (Ponomarenko, 1984, 1985, 1992, 1996; Makarkin, 1990; Engel and Grimaldi, 2008; Khranov, 2011), or considered as *familia incertae sedis* (Carpenter, 1992; Jepson et al., 2012).

Three other Jurassic species were assigned to this genus: *Liassopsychops altaicus* Ponomarenko, 1984 (Lower/Middle Jurassic of Oshin-Boro-Udzyur-Ula, Mongolia (Zhargalant Formation)), *L. sibiricus* Ponomarenko, 1984 (Lower/Middle Jurassic of Vladimirovka on the Iya River, Irkutsk Oblast', Russia (Cheremkhovo Formation)), and *L. makulbekovi* Ponomarenko, 1992 (Middle/Upper Jurassic of Bayan-Teg, Mongolia). However, this generic placement is certainly incorrect as their venation strongly differs from that of two specimens of *Liassopsychops curvatus* described below. We agree with Khranov (2017) that all these species probably belong to different genera and even families.

*Liassopsychops curvatus* Bode, 1953  
(Figs. 3–6, 8A, B, 9)

1953 *Liassopsychops curvata* – Bode, p. 248, pl. 12, fig. 321.

1984 *Liassopsychops curvata* Bode – Ponomarenko, p. 67.

1996 *Liassopsychops curvata* Bode – Ponomarenko, p. 78, figs. 8, 22.

2001 *Liassopsychops curvata* Bode – Andersen, p. 432.

**Type material:** Holotype: CI 279, current location unknown, formerly deposited in TUPCI. An apical portion of a forewing with a rather well-developed apical eye-spot.

**Material examined:** Specimen MK-0015-In, collected in the spring of 1987 by Michael Klopschar (Braunschweig, Germany) and deposited in his private collection. An almost complete forewing, Schandelah in the vicinity of Braunschweig, Lower Saxony, Germany. Lower Jurassic: lower Toarcian, uppermost *elegantulum* subzone. Specimen BSPG 2009/XIX, 11, deposited in BSPG. A nearly complete forewing, Kerkhofen, Bavaria, Germany. Lower Jurassic: lower Toarcian, uppermost *elegantulum* subzone.

**Type locality and horizon:** Germany: Lower Saxony (Niedersachsen): Grassel, near Braunschweig. Lower Jurassic (lower Toarcian), uppermost *elegantulum* subzone.

**Description:**

Specimen MK-0015-In (Figs. 4, 8A). Forewing 73 mm long as preserved (estimated complete length 75 mm), ca. 33 mm wide. Trichiation on veins not discernible. Trichosors poorly preserved, even along well-preserved costal margin. Costal space proximally dislocated; moderately broad, slightly narrowed towards wing apex. Most subcostal veinlets dichotomously branched, connected by one to five crossveins not forming regular costal series in proximal and medial part. Humeral veinlet not preserved. Subcostal space relatively broad, narrowed distally, with rather closely-spaced

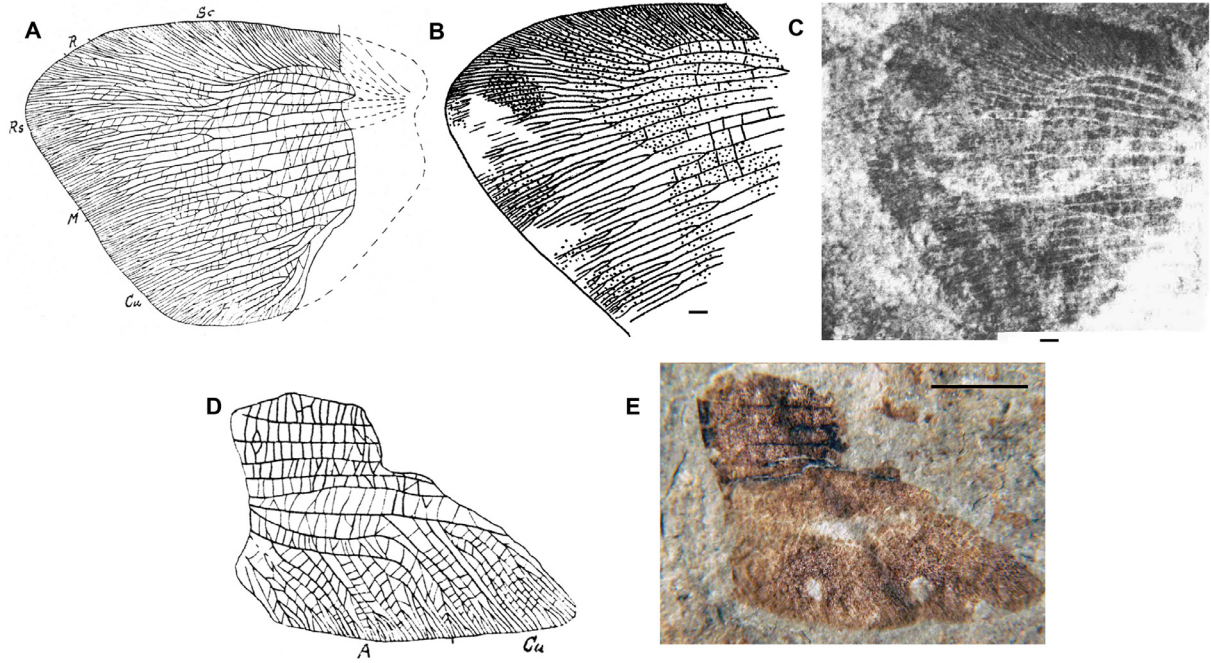


Fig. 3. *Liassopsychops curvatus* Bode, 1953. (A–C) Holotype; (A) original drawing of Bode (1953, pl. 12, fig. 321); (B) drawing of Ponomarenko (1996); (C) photograph of Ponomarenko (1996). (D, E) Specimen Hi 21; (D) original drawing of Bode (1953, pl. 12, fig. 322); (E) photograph. Scale bar = 1 mm for (B, C), 5 mm for (E).

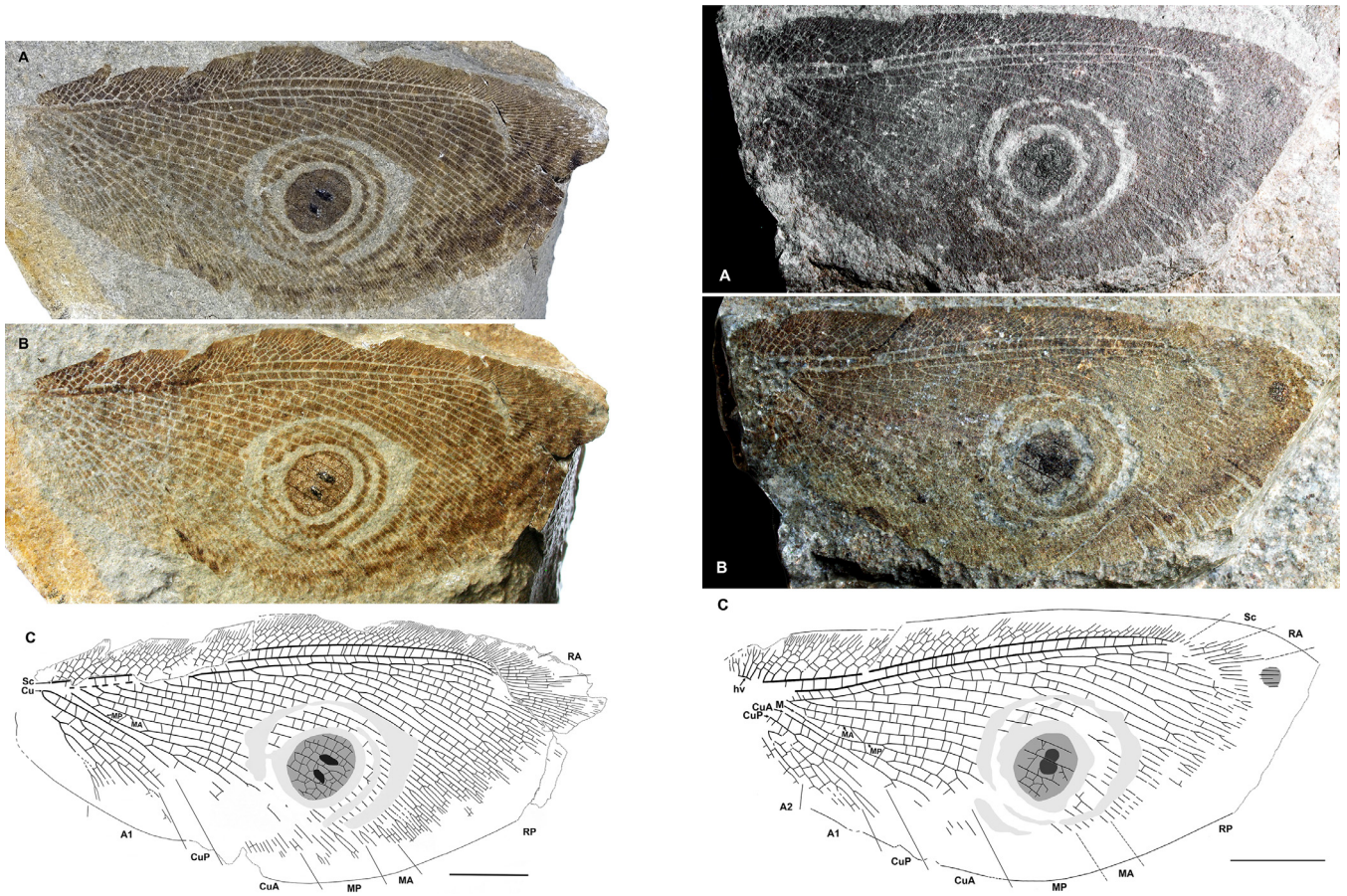


Fig. 4. *Liassopsychops curvatus* Bode, 1953, MK-0015-In, specimen as preserved. (A) Dry. (B) Wetted with ethanol. (C) Forewing venation. Scale bar = 10 mm (all to same scale).

Fig. 5. *Liassopsychops curvatus* Bode, 1953, BSPG 2009/XIX, 11, specimen as preserved. (A) Dry. (B) Wetted with ethanol. (C) Forewing venation. Scale bar = 10 mm (all to same scale).

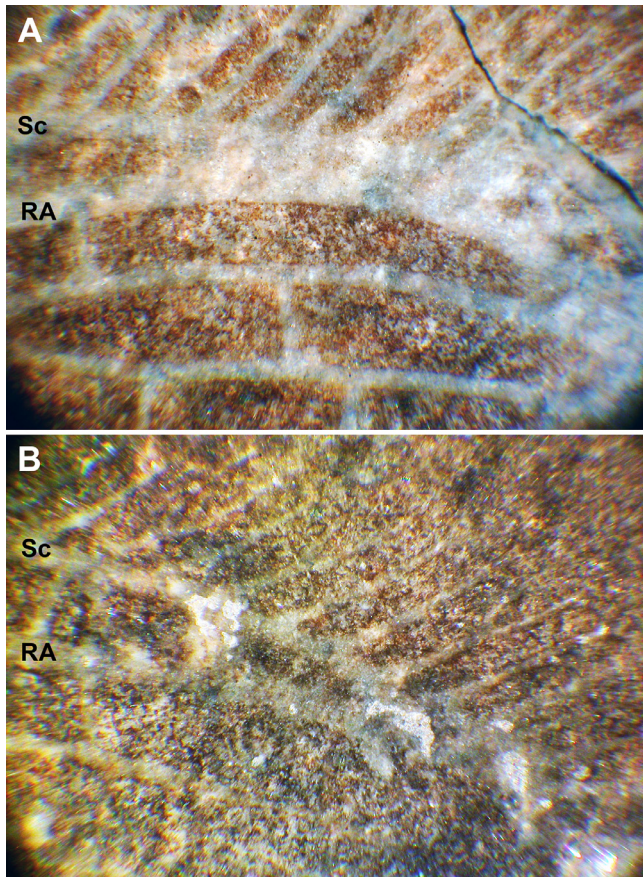


Fig. 6. *Liassopsychops curvatus* Bode, 1953, relationships of distal parts of Sc and RA in the forewing (not to scale). (A) MK-0015-In. (B) BSPG 2009/XIX, 11.

crossveins. Sc and RA rather stout, distally not fused. RA distally dichotomously forked, with two dichotomously forked branches. RA space slightly narrower than subcostal space, with numerous crossveins. RP originating close to base of wing, with 12 branches; RP1–RP5, RP11, RP12 shallowly dichotomously forked; RP6–RP10 deeply dichotomously forked. Interrelationships of basal M and R unclear. M forked rather close to wing base; MA shallowly dichotomously branched; MP in general dichotomously branched with two deep forks. Cu divided into CuA and CuP very close to base of wing. CuA in general dichotomously branched, with two long pectinate branches (distal portion poorly discernible). Dichotomous branching of CuP similar to that of MP, deeply forked twice (distal portion not discernible). A1 profusely dichotomously branched. A2 and A3 not discernible. Wing posterior to RP filled with rather widely spaced crossveins (compared with most other Kalligrammatidae); crossveins in area of marginal twigging more widely spaced. Jugal lobe not detected. Wing membrane in general dark, with veins appearing pale. Numerous elongate dark-brown patches along posterior and apical margins; darkest oval patch at apical-most edge, which is apparently not apical eye-spot. Central eye-spot distinct, consisting of central rounded dark structure (central pigmented disc), with two well-sclerotized (blackish) kidney-shaped spots (swellings), and two pale complete rings around this structure

(outer rings); incomplete third ring between them. Veins of MA and three proximal RP branches inside central pigmented disc well discernible, dark-brown.

Specimen BSPG 2009/XIX, 11 (Figs. 5, 8B, 9). Forewing 63 mm long, 28.5 mm wide. Trichiation on veins not discernible. Trichosors very poorly preserved. Costal space moderately broad, widest at proximal 1/6 of length, slightly narrowed towards wing apex. Subcostal veinlets dichotomously branched in proximal half, incompletely preserved in distal half; connected by one to five crossveins not forming regular costal series. Humeral veinlet partly preserved, recurrent, with six (or more) branches, mostly forked. Subcostal space relatively broad, narrowed distally, with rather closely-spaced crossveins. Sc and RA probably not fused distally. RA distally with three dichotomously forked branches. RA space slightly narrower than subcostal space, with numerous crossveins with anterior apex inclined toward base. RP originating close to base of wing, with ten branches; RP1–RP5 shallowly dichotomously forked; RP6–RP10 deeply dichotomously forked. M forked rather close to base of wing; MA shallowly dichotomously branched (proximal-most forking located in central rounded dark structure of eye-pot); MP in general dichotomously branched, deeply forked two times (distal portion not discernible). Cu probably divided into CuA and CuP very close to base of wing (fork not preserved). CuA dichotomously branched, with three deep forkings. CuP dichotomously branched, deeply forked three times (distal portion not discernible). A1 profusely dichotomously branched. A2 only partially preserved. A3 not discernible. Wing posterior to RP filled with rather widely spaced crossveins, which in distal areas more widely spaced or not detected. Wing membrane in general dark, darker along outer and posterior margins; veins appearing pale. Apical eye-spot distinct, rounded, dark-brown, consisting only of a central pigmented disc (Fig. 8C). Central eye-spot distinct, consisting of central pigmented disc; two darker, large and indistinct swellings in centre; and two pale nearly complete outer rings around central pigmented disc (there is a fragment of a third outer ring beyond them). Veins of MA and three proximal RP branches inside central pigmented disc of both central and apical eye-spots well discernible, dark-brown.

**Remarks:** Bode (1953) described this species based on two specimens, CI 279 designated as the holotype. Ponomarenko (1996) re-described this specimen (Fig. 3A–C). The second specimen (Hi 21) is a small wing fragment (Fig. 3D, E). Ponomarenko (1996) suggested that it is provisionally the same species, but he misreported it as specimen Ma 14504 (see Ponomarenko, 1996, p. 78). The actual specimen Ma 14504 is deposited in Niedersächsisches Landesamt für Bodenforschung (Hannover, Germany), a complete neuropteran wing (about 9.5 mm long) probably belonging to the genus *Actinophlebia* Handlirsch, 1906 (*Osmylopsychoptidae?*). It was collected by Wunnenberg in Hattorf in 1964. Specimen Hi 21 is regarded here as *Kalligrammatidae incertae sedis*, as it lacks sufficiently distinctive characters to assign it to a genus or species.

The holotype cannot be examined, as it was not properly returned from a loan to the Paleontological Institute (Moscow)

and its current whereabouts is unknown. Judging from Ponomarenko's figures, however, the two complete forewings that we describe here are likely conspecific, being of the same age and locality, and having a similar size, preserved venation, and location of the apical eye-spot as the holotype (see Fig. 3A–C). However, the holotype is so fragmentary that this determination would necessarily be provisional. They differ in that the apical eye-spot is apparently not developed in MK-0015-In, but is distinct in the holotype and BSPG 2009/XIX, 11. Further, the two swellings in MK-0015-In are well developed, but are indistinct in BSPG 2009/XIX, 11. These differences might, however, be explained by sexual dimorphism: MK-0015-In may be a male, and the holotype and BSPG 2009/XIX, 11 females (see below).

Specimen BSPG 2009/XIX, 11 was previously reported as belonging to the Psychopsidae (Tischlinger, 1992, fig. 50) and the Kalligrammatidae (Makarkin et al., 2009, p. 964; Nose, 2010, fig. 4), and specimen MK-0015-In as a member of the Kalligrammatidae (Klopschar, 2006, fig. 19.19; Ilger, 2014, fig. 28).

#### Subfamily Kallihemerobiinae Ren and Engel, 2008

2001 Kallihemerobiidae – Ren, p. 58 (*nomen nudum*).

2008 Kallihemerobiinae – Ren and Engel, 2008, p. 167.

**Emended diagnosis:** Mouthparts siphonate (1); both fore- and hind wings with several (three to > 26) branches of RP originating separately on RA (ORBs) (2), and MP with several pectinate anteriorly-directed branches (3); forewing CuA branched only distally (4); hind wing CuA strongly pectinate, often for most length (5); forewing CuP pectinate (6); hind wing CuP dichotomous (7); central eye-spot possesses oculus surrounding central pigmented disc in both wings (8).

**Genera included:** *Ophthalmogramma* n. gen., *Kallihemerobius* Ren and Oswald, 2002, *Apochrysogramma* Yang et al., 2011, and *Affinigramma* Yang et al., 2014b.

**Occurrence:** Lower Jurassic (lower Toarcian) of Europe (Germany) to Middle/lowermost Upper Jurassic of China (Daohugou).

**Remarks:** We consider Kallihemerobiinae generally as defined by Yang et al. (2011), emended here (see diagnosis). The forewing character states of *Ophthalmogramma* n. gen. agree with the diagnosis of the subfamily by characters (2) – (4) and (8).

Yang et al. (2014b) included seven genera in the subfamily, i.e., *Kallihemerobius*, *Apochrysogramma*, *Affinigramma*, *Huiyingogramma*, *Kalligrammula* Handlirsch, 1919, *Lithogramma* Panfilov, 1968, and *Stelligramma* Yang et al., 2014b. They declared that “the deep MA [our RP1] bifurcation indicates monophyly of the Kallihemerobiinae” (Yang et al., 2014b, p. 4). However, this character state alone is very weak to establish monophyly. The general venation of the four genera (*Huiyingogramma*, *Kalligrammula*, *Lithogramma*, *Stelligramma*) differ significantly from each other and from the other three genera as a group (*Kallihemerobius*, *Apochrysogramma*, *Affinigramma*). The former four genera are certainly

distantly related to the latter three, and the subfamily sensu Yang et al. (2014b) is, therefore, clearly paraphyletic. Indeed, *Huiyingogramma* is quite different from other genera; here, we assign it to Liassopsychopinae n. subfam. (above). The genus *Limnogramma* (Kalligrammatinae) was later synonymized with *Kalligrammula* (Liu et al., 2015), both belonging to the Kalligrammatinae. *Lithogramma* and *Stelligramma* are represented by incomplete specimens, and their subfamily affinity remains uncertain.

Genus *Ophthalmogramma* n. gen.

**Type and only species:** *Ophthalmogramma klopschari* n. sp.

**Etymology:** From the Greek *ophthalmos*, eye, and *-gramma*, a traditional ending of generic names in Kalligrammatidae (from the Greek *gramma*, *-atos*, mark, drawing, letter), referring to the presence of an eye-spot on a wing. Gender neuter.

**Diagnosis:** Presumable forewing with (1) distal ORB (proper RP) bearing three branches (seven in *Affinigramma*); (2) branches of RP and M closely spaced (widely spaced in *Kallihemerobius*); (3) MP with  $\geq 10$  branches (maximum eight in *Kallihemerobius* and *Affinigramma*); (4) outer gradate series present (absent in other genera).

**Remarks:** The venation of *Ophthalmogramma* n. gen. is most similar to that of *Apochrysogramma*, sharing characters (1) to (3). The structure of the central eye-spot of both genera is also similar, particularly by the presence of numerous small oculus and one or two large embossed areas (swellings) in the center.

*Ophthalmogramma klopschari* n. sp.

(Figs. 7, 8C, D)

**Etymology:** The species is named in honor of Michael Klopschar (Braunschweig), the collector of the specimen, in recognition of his support of this study.

**Type material:** Holotype SNHM-3425-In, collected in the spring of 1987 by Michael Klopschar (Braunschweig, Germany) and deposited in SNHM. A fragment of a forewing with an eye-spot.

**Type locality and horizon:** Germany: Lower Saxony (Niedersachsen): Schandelah, near Braunschweig, former marl pit, Lower Jurassic (Lower Toarcian), *boreale* nodule, uppermost *elegantulum* subzone.

**Description:** Forewing fragment ca. 20 mm long, ca. 17 mm wide as preserved (estimated complete length 30–35 mm, width 18 mm). Costal space in apical portion very broad. Subcostal veinlets closely spaced, mostly forked (their terminals poorly preserved); between them few crossveins detected. Margins not or poorly preserved, so trichosors not detected. RA terminates on Sc far from wing apex. Distal part of subcostal space narrow, with few crossveins detected. Distal portion of RP with two branches separately originating on RA (ORBs): distal-most ORB (RP proper) rather long, with three branches; ORB located proximad RP proper, probably not deeply forked. Basal parts of other 15 branches of RP not preserved. All branches of RP forked in distal parts, one to three times. Low-forked presumptive MA with two distal branches. Posterior trace of MP probably with many (ten or more)

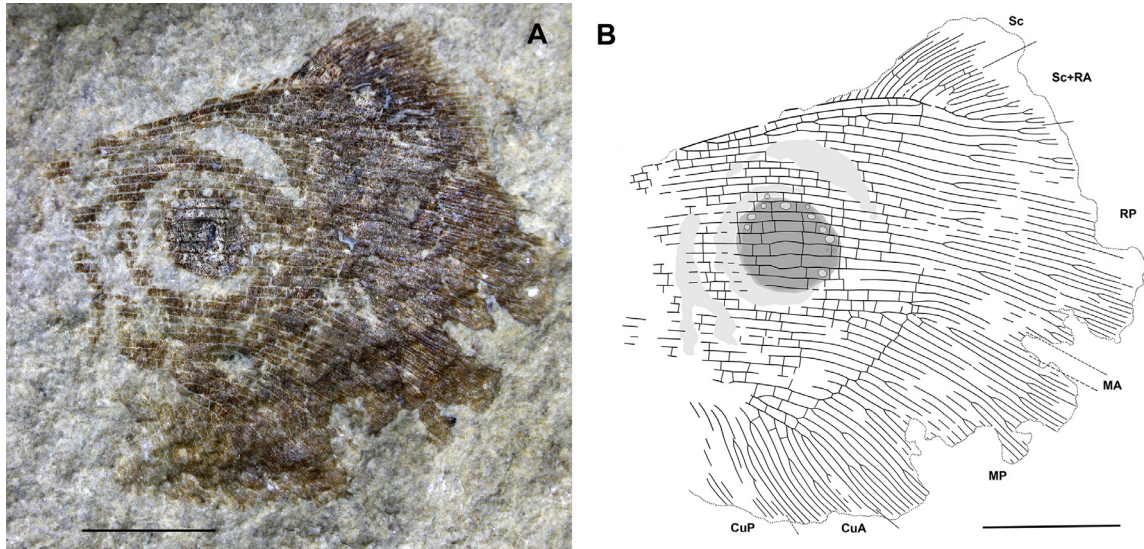


Fig. 7. *Ophthalmogramma klopschari* n. gen. n. sp., holotype SNHM-3425-In. (A) Specimen as preserved, wetted with ethanol. (B) Forewing venation. Scale bar = 5 mm.



Fig. 8. Central eye-spots of the lower Toarcian Kalligrammatidae. (A, B) *Liassopsychops curvatus* Bode, 1953; (A) MK-0015-In; (B) BSPG 2009/XIX, 11. (C, D) *Ophthalmogramma klopschari* n. gen. n. sp., holotype SNHM-3425-In; (C) dry; (D) wetted with ethanol. Abbreviations: cpd, central pigmented disc; oc, oculus; or, outer ring; sw, swelling. Scale bar = 5 mm for (A, B), 1 mm for (C, D).

pectinate anteriorly-directed branches; proximal-most branch with four pectinate posteriorly-directed branches; all branches forked at or distad outer gradate series, one to two times. Distal part of CuA parallel to MP, with probably seven pectinate branches, each forked once; few crossveins between them, only near their origins. CuP fragmentarily preserved. Anal veins not preserved. Crossveins in radial to medial spaces numerous, comparatively widely spaced, mostly irregularly arranged; distal crossveins form outer gradate series, well discernible from posterior branches of RP to CuA; clearly-discernible crossveins distad this series not detected. Wing membrane generally dark. Central eye-spot well developed: a darkish rounded central pigmented disc (approximately 3 mm in diameter) within two convex (embossed) areas (swellings) and transverse black stripe (this may be an artifact); many (approximately eleven in number) smaller pale spots (ocules) differing in size (diameter from 0.1 mm to 0.4 mm), forming ring around central pigmented disc; each pale spot located in one cell, whereas central pigmented disc occupying many cells; two incomplete pale outer rings around central pigmented disc and ocales (inner ring nearly complete, approximately 5 mm in diameter; outer ring very incomplete).

**Remarks:** This wing is interpreted as a forewing due to the branching of CuA: anterior apices of proximal-most branches are clearly inclined to the base and most probably belong to CuP, while the hind wing CuA is pectinately branched for most of its length in all Kallihemeroptera. Such a distal branching of CuA is characteristic of the forewing in all Kallihemeroptera.

A distally pectinately-branched vein is interpreted as the proximal branch of MP as this condition often occurs in other Kallihemeroptera (see e.g., Yang et al., 2014b, fig. 4C).

## 5. Discussion

### 5.1. Paleoclimatic conditions in the early Toarcian

It is now well established that the climate in the Early Jurassic dramatically changed from temperate to hot greenhouse (even super-greenhouse) during the Pliensbachian–Toarcian interval (e.g., Hermalso et al., 2013; Hesselbo et al., 2013; Slater et al., 2019; van de Schootbrugge et al., 2019). The early Toarcian is the warmest interval of the Jurassic Period, with an abrupt rise in global temperatures of up to  $\sim 7^{\circ}\text{C}$  in mid-latitudes at the onset of the Toarcian Oceanic Anoxic Event (Xu et al., 2018b). This global warming is thought to have been caused by volcanogenic outgassing of  $\text{CO}_2$  during Karoo–Ferrar igneous province eruptions (Pálffy and Smith, 2000; Caruthers et al., 2014) and the release of thermogenic and/or biogenic methane (Slater et al., 2019). The Toarcian thermal optimum is easily traceable by physico-chemical evidence in marine sediments including a high total organic carbon content (e.g., Xu et al., 2018b), and by the taxonomic composition of plant communities almost throughout Eurasia (Vakhrameev, 1988). Even in northern Siberia (i.e., in the Arctic), this warming on land was relatively rapid. The abundance of pollen of *Classopollis* (cheirolepid coniferans) and other thermophile plants was observed in this region in the lower

Toarcian from the end of the *antiquum* (= *tenuicostatum*) zone to the middle of *commune* zone (Zakharov et al., 2006; Suan et al., 2011).

In the early Toarcian, middle and western Europe was situated between palaeolatitudes  $30^{\circ}\text{N}$  and  $40^{\circ}\text{N}$  (Xu et al., 2018a), and included several large massif islands and smaller islands (Fig. 1). Unfortunately, the terrestrial biota of these islands is only known by fossils from marine sediments, often deposited far from shore and so subject to the associated taphonomic sorting.

Plant remains are comparatively rare in the Posidonia Shale. These include undetermined Equisetales, two species of conifers and four species of *Bennettitales* (Keller and Wilde, 2000; Wilde, 2001). Conifers are represented by twigs referred to the formal genera *Pagiophyllum* and possibly *Bra-chyphyllum*, both belonging to Cheirolepidiaceae which produce *Classopollis* pollen (Vakhrameev, 1988). Palynological investigations of the Hondelage section near Schandelah revealed a rather poor terrestrial plant association, dominated by gymnosperm pollen of *Classopollis*, *Chasmatosporites* (cycads) and *Cerebropollenites* (cupressaceans). Together with rare fern spores and macrospores this indicates a warm and relatively dry climate (Heunisch, 2014). Similarly, vegetation in England in that time was represented by a low-diversity assemblage dominated also by cheirolepid conifers, cycads and *Cerebropollenites*-producers, which were able to survive in warm and arid conditions (Slater et al., 2019).

Therefore, the oldest known kalligrammatids lived in warm and relatively dry conditions.

### 5.2. The early Toarcian Kalligrammatidae

The occurrence of two distantly-related genera of Kalligrammatidae representing two different subfamilies in the lower Toarcian is unexpected. It implies that the diversity of this family in that time was already high. Its diversification was probably initiated by the Toarcian “super”-greenhouse climate, but the family certainly originated earlier, possibly in the Late Triassic or the earliest Jurassic.

The closest relatives of Kalligrammatidae are the Triassic to Early Cretaceous Osmylopsychoptera and the Jurassic Parakseneuridae. The venation of the genus *Petropsychoptera* Riek, 1956 (Osmylopsychoptera) from the Upper Triassic of Australia is most similar to that of many Kalligrammatidae, especially by the configuration of their M (see Lambkin, 2014, fig. 9). The size and venation of *Parakseneura* Yang, Makarkin and Ren in Yang et al., 2012 (Parakseneuridae) from the Middle/lowermost Upper Jurassic of China are very similar to those of the kalligrammatid genus *Protokalligramma* which bears the most generalized venation in the family (cf. Yang et al., 2011, fig. 2 and Yang et al., 2012, figs. 1, 6). The forewing venation of the Toarcian *Liassopsychoptera* is in general similar to that of *Protokalligramma*, indicating that the ancestors of Kalligrammatidae were probably parakseneurid-like Neuroptera. However, the occurrence of *Ophthalmogramma* n. gen. in the lower Toarcian with its derived forewing does not fit this pattern. *Liassopsychoptera* probably continues the main

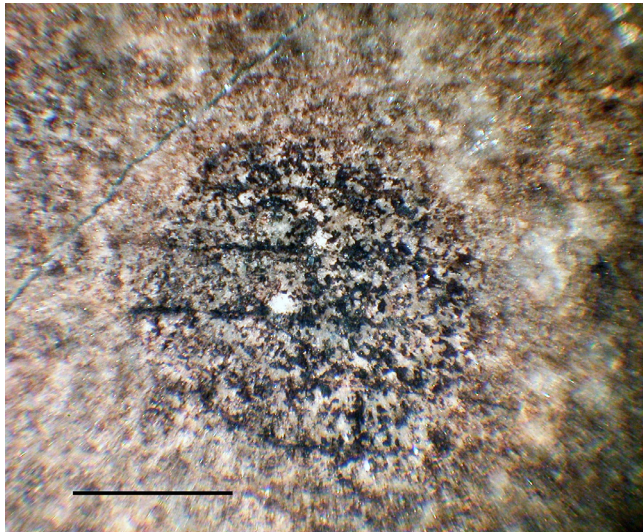


Fig. 9. Apical eye-spot of *Liassopsychops curvatus* Bode, 1953, BSPG 2009/ XIX, 11. Scale bar = 1 mm.

lineage leading from parakseneurid-like Neuroptera to Kalligrammatidae, as its venation has changed little, with *Ophthalmogramma* n. gen. (and Kallihemerobiinae) as a side branch of early Kalligrammatidae.

*Paractinophlebia curtisii* (Scudder, 1886) from the lower Toarcian of Alderton (England) was considered to belong to the Kalligrammatidae by Whalley (1988) and Ross and Jarzembowski (1993). However, examination of high-resolution photographs of the holotype shows that this species probably belongs to an undescribed Mesozoic family (“Familia nova A”: Makarkin et al., 2012, p. 63), but certainly not to Kalligrammatidae. The holotype is a fragment of a hind wing (most probably), which is strongly dissimilar to wings of Kalligrammatidae, in particular by the presence of rare crossveins arranged in series and by the very narrow subcostal space (VM, pers. obs.).

The Toarcian Kalligrammatidae are currently only known from deposits with insects originating from the Bohemian Massif or an offshore island (see Fig. 1). They are currently unknown from northern localities in Germany (Dobbertin, Grimmen) and England. This may be a result of collecting or taphonomic biases, but more probably explained by paleoclimatic reasons. This would be consistent with large neuropterans with forewing length more than 5 cm being restricted to southern localities of the region. *Titanoptilon brunsvicense* Bode, 1953 and *Panfilovia fasciata* Ponomarenko, 1996, both from Hondelage, have estimated wing lengths of 50 mm. Similar large-sized neuropteran wings are known from Kerkhofen (collection of Brachert in Staatliches Museum für Naturkunde, Stuttgart, and the collection of Hartwig in Bayerische Staatssammlung für Geologie und Paläontologie, Munich).

The absence of Toarcian kalligrammatids in higher latitude localities (Dobbertin, Grimmen) might also be explained by different plant associations, as has been proposed to explain the distribution of plant-sucking fulgoromorphs (Homoptera) in German Toarcian localities (Ansorge, 2003).

As aforementioned, the Toarcian Kalligrammatidae lived in warm and dry conditions. In general, the family is considered thermophilic, as they were not distributed in the Jurassic and Cretaceous in the cooler Siberian floristic region (Khramov, 2014; Bechly and Makarkin, 2016). They occur only in localities where pollen grains of *Classopollis* — an indicator of dry conditions — are abundant, except for the Lower Cretaceous Yixian Formation (northeastern China) where their presence is low (Li and Batten, 2007). The Yixian Formation climate was mostly “warm and seasonal, with fairly short wet phases and longer dry (arid) periods” (Li and Batten, 2007, p. 337). Therefore, kalligrammatids were not only thermophilic, but also relatively xerophilic.

Bennettitales were diverse, but infrequent in the Posidonia Shale; their reproductive organs might be a food source for kalligrammatids. Unfortunately, the mouthparts of both Toarcian kalligrammatid species are unknown, but other known Jurassic Kallihemerobiinae had proboscises of 9.1–13.9 mm in length (Liu et al., 2018).

The Kalligrammatidae were the largest Toarcian insects in Europe along with some campteropteriid damsel-dragonflies (e.g., *Campteropteria elegans* Bode, 1905) whose wing length reached 73 mm. They were probably too big to be preyed upon by other insects, but vertebrates could have fed on them, perhaps including the pterosaurs *Campylognathoides* Strand, 1928 and *Dorygnathus* Wagner, 1860, known from the Toarcian, mostly from the Posidonia Shale of Holzmaden, which had wing spans of 1.75 m and 1 m, respectively (Padian, 2008). A hip of *Campylognathoides* sp. was described from Schandelah by Wellnhofer and Vahldieck (1986). Although both pterosaurs are commonly thought to have been piscivorous, it may well be imagined that they also fed on insects (for a review of pterosaur diets see Bestwick et al., 2018).

Small terrestrial microvertebrates are described from the Lower and Middle Jurassic of the United Kingdom (Evans and Kermack, 1994; Evans and Milner, 1994); however, nothing is known about small Toarcian terrestrial tetrapods. The only known lizard from Posidonia shale, *Palaeopleurosaurus posidoniae* Carroll, 1985 (Sphenodontia) is thought to have been aquatic (Klein and Scheyer, 2016).

### 5.3. The structure of wing eye-spots in Kalligrammatidae

The presence of a large, central eye-spot on both fore- and hind wings of most Kalligrammatidae is a characteristic feature of this family. These eye-spots are diverse in structure. Labandeira et al. (2016) classified five types, but we find this unsatisfactory and partially incorrect. Type 5 of *Kallihemerobius aciedentatus* is called simply a “spot”, as this is a simple circular pigmented central disc, without oculus and outer rings (Labandeira et al., 2016, fig. 1q). However, the photograph of this was taken from the part of the right forewing, whereas on the counterpart, it has a number of vaguely discernible oculus (pers. obs.). Moreover, seven oculus are well discernible in the hind wing eye-spot of this counterpart, and in general it is very similar to the eye-spot of *Kallihemerobius feroculus*, i.e., to Type 2. Therefore, Labandeira et al. (2016) actually

determined at most four types of eye-spots; however, these are not strongly defined, and there are intermediate conditions.

We found that at least one specimen of Kalligrammatidae — BSPG 2009/XIX, 11 of *Liassopsychops curvatus* — possesses two eye-spots, central and apical (Figs. 8B, 9). The central eye-spot is characterized by the following four main components.

(A) A dark rounded central part ('pupil' of Jarzembowski (2001), 'central pigmented disc' of Labandeira et al. (2016)) is present in all species of Kalligrammatidae. We accept this term. The central pigmented disc is usually flat, but is clearly embossed in the center in *Apochrysogramma rotundum* Yang et al., 2011 (fig. 6A). However, this embossed central part may be actually a swelling (see below).

(B) Two distinct elongate embossed structures in the central pigmented disc, called 'swellings' by Jarzembowski (2001) are detected in MK-0015-In of *Liassopsychops curvatus* (Fig. 8A), the holotype of *Huiyingogramma formosum* (Liu et al., 2014, fig. 2), and in a new species of *Huiyingogramma* (V.M., pers. obs.). These swellings are very indistinct in *H. turutanovae*; this area appears nearly like that of specimen BSPG 2009/XIX, 11 of *L. curvatus* (see Fig. 8B).

Rounded swellings are present in Kalligrammatinae: there are three in the hind wing of *Kalligrammula hani* (Makarkin et al., 2009) (Makarkin et al., 2009, fig. 2A); one large central swelling in the forewing of *Kalligramma elegans* (Yang et al., 2014a, fig. 2A), and four small oval swellings in *K. roycrowsoni* Jarzembowski, 2001 (see Jarzembowski, 1984, fig. 36). Two swellings in *Ophtalmogramma* n. gen. are indistinct and large (see Fig. 8C). Swellings in most other species are possibly present, but not detected due to poor preservation.

(C) There are small pale rounded spots surrounding the central pigmented disc in many species, from seven to 35, called 'ocules' by Labandeira et al. (2016) (see Fig. 8D). Clearly discernible ocales occur for example in all genera of Kallihemerobiinae, including *Ophtalmogramma* (except *Affinigramma* in which these are not detected, probably due to poor preservation); *Oreogramma illecebrosa* Yang et al., 2014b; and *Kalligramma elegans* Yang et al., 2014a. The detection of ocales in many cases depends on the state of preservation of the specimen. We may be sure that ocales are absent only in a small number of well-preserved specimens, e.g., MK-0015-In of *Liassopsychops curvatus*.

(D) Outer rings (the term of Labandeira et al., 2016) surrounding the central pigmented disc and ocales are also characteristic of most species. These are usually pale (white or grey), rarely dark, one to three in number. Every species has a characteristic configuration of these rings.

The apical eye-spot is detected only in two specimens of *Liassopsychops curvatus*, its holotype and BSPG 2009/XIX, 11. It consists of only the central pigmented disc (Fig. 9).

Central eye-spots may be reasonably classified by the presence/absence of these four components. The structure of the central eye-spot in *Makarkinia* Martins-Neto, 1997, which has no swellings and no ocales (type A-D), appears simplest. Its central pigmented disc is surrounded only by outer rings, broad and pale inner-most, then three dark brown and closely spaced, whose colorations are much darker than the background of the

wing (Bechly and Makarkin, 2016, fig. 4). On the other hand, the central eye-spot of many species (including *Ophtalmogramma klopschari* n. sp.) possess all four components (type A-B-C-D). The central eye-spot of *Liassopsychops curvatus* is accordingly type A-B-D.

*Makarkinia* is the youngest known genus of Kalligrammatidae and *Ophtalmogramma* is one of the oldest. Therefore, complexity of the central eye-spot did not increase with time. Both early Toarcian genera of Kalligrammatidae have a complex structure of their central eye-spots.

The kalligrammatid central eye-spot is usually thought to function either to intimidate or distract predators as in some Lepidoptera (Labandeira et al., 2016).

The function of the swellings in the central eye-spot is unclear. Their apparent differential development in similar species may actually be sexual dimorphism. For example, in *Liassopsychops curvatus*, MK-0015-In possesses two well-developed swellings and the apical eye-spot is not clearly formed (possibly absent), while the swellings in BSPG 2009/XIX, 11 are not clear, but the apical eye-spot is well developed. If we assume that MK-0015-In is a male, and BSPG 2009/XIX, 11 a female, then swellings may serve as a pheromone container and the apical eye-spot as a pheromone detector in this species (in other species a pheromone detector might be located elsewhere). Similarly, pheromone containers are present on wings of some male Trichoptera (as a corema), e.g., the early Toarcian *Liadotautilus* Handlirsch, 1939; the extant *Apsilochorema* Ulmer, 1907 (see Mey, 1999; Ansoerge, 2002). However, this hypothesis should be a matter of further research on new and well-preserved material.

## Acknowledgements

We thank the following people for various help: Michael Klopsch (Braunschweig) for allowing us to study the Schandelah specimens and providing additional information on the Schandelah and Hondelage sections; Mike Reich (BSPG) for allowing us to study the Kerkhofen specimen; Jürgen Vespermann (Roemer-Paelliceus Museum Hildesheim), Carmen Heunisch (Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover) and Günther Schweigert (Staatliches Museum für Naturkunde, Stuttgart) for photographs of specimens under their care; Dmitry E. Shcherbakov (Palaeontological Institute, Moscow), Carsten Brauckmann (TUPCI), and Alexander Gehler (University of Göttingen) for information on the Bode types; Claire Melish (Natural History Museum, London) for photographs of *Paractinophlebia curtisii*; Qiang Yang (Guangzhou University, China) for photographs of some species of Kalligrammatidae from the Chinese Mesozoic; Bruce Archibald (Simon Fraser University Canada) for editing of the English; and Bo Wang and an anonymous reviewer for providing valuable suggestions to improve this manuscript.

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