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The Coleorrhyncha (Insecta: Hemiptera) of the European Jurassic, with a description of a new genus from the Toarcian of Luxembourg

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Key words: *Indutionomarus treveriorum* gen. et sp. nov., *Mesocimex anglicus* (Yu. Popov, Dolling et Whalley) comb. nov., Toarcian Oceanic Anoxic Event, taxonomy, phylogeny, palaeoclimate, palaeoenvironment.

Abstract. The fossil record of the Coleorrhyncha goes back to the Upper Permian. In recent faunas only members of the Peloridiidae are present, restricted in distribution to the Southern Hemisphere. These insects were more diversified in the past, and though their fossil record in the Jurassic is restricted to the Northern Hemisphere, it comprises the families Progonocimicidae and Karabasiidae. The subfamily Progonocimicinae, present in the Jurassic strata of Europe and Asia is a declining lineage. The subfamily Cicadocorinae originated at the Triassic/Jurassic boundary and became dominant during Jurassic times. A review of Coleorrhyncha from European fossil sites is given, with taxonomic and phylogenetic problems highlighted. Their occurrence is linked to a very humid and warm climate, which is in agreement with independent data indicating greenhouse conditions in the atmospheric system and anoxia in the oceans at that time (Toarcian-Oceanic Anoxic Event – T-OAE) and coeval greenhouse climate on land. A new genus and species of the Progonocimicinae – *Indutionomarus treveriorum* **gen. et sp. nov.** is described, based on a specimen from the Lower Toarcian of Bascharage, Luxembourg, Western Europe. It is the first record of the Coleorrhyncha from this locality. The morphological features of the new genus in respect to other Progonocimicidae, and its phylogenetic importance, are discussed. *Mesoscytina anglica* Yu. Popov, Dolling et Whalley, 1994 is transferred to the genus *Mesocimex*, resulting in *Mesocimex anglicus* (Yu. Popov, Dolling et Whalley, 1994) **comb. nov.**

INTRODUCTION

Though the diminutive members of the suborder Coleorrhyncha are small in number of species they comprise an interesting and phylogenetically very important suborder of the Hemiptera. They were regarded as the most remarkable of all the Hemiptera (Helmsing, China, 1937). The Coleorrhyncha are famous because of their long evolutionary history, interesting morphological and behavioral features and the limited distribution of recent representatives (Evans, 1982; Popov, Shcherbakov, 1991, 1996; Burckhardt, Agosti, 1991; Burckhardt, 2000, 2009; Grimaldi, Engel, 2005; Hoch *et al*., 2006; Burrows *et al*., 2007; Wang *et al*., 2009; Burckhardt *et al*., 2011; Szwedo *et al*., 2011). The Coleorrhyncha contains three families: the recent Peloridiidae Breddin, 1897 and the extinct Karabasiidae Yu. Popov, 1985 within the Peloridioidea Breddin, 1897, and the extinct Progonocimicidae Handlirsch, 1906 within the Progonocimicoidea Handlirsch, 1906. The phylogenetic relationships of the Coleorrhyncha are of particular interest. Originally, Breddin (1897) described them in the Heteroptera; later this group was postulated to be placed in the 'Homoptera' (Myers, China, 1929; Woodward, 1956; China, 1962; Pendergrast, 1962; Evans, 1963, 1967; Estevez, de Remes Lenicov, 1990; Burckhardt, Agosti, 1991). These options which coexisted for a long time were summarized by Evans (1982), who concluded that the available evidence seems inadequate to associate the recent Peloridiidae (therefore the Coleorrhyncha) with either the 'Homoptera' or the Heteroptera. It must be noted that 'Homoptera', once believed to be a monophylum, is in fact

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a paraphyletic assemblage (von Dohlen, Moran, 1995; Sorensen *et al*., 1995; Brożek *et al*., 2003; Szwedo *et al*., 2004) and as a result, the taxon name 'Homoptera' became abandoned (Gullan, 1999). Other authors regarded the Coleorrhyncha as a sister taxon to the Heteroptera, and the latter statement was proved by several molecular phylogenetic studies and morphological evidence (Schlee, 1969; Wheeler *et al*., 1993; Campbell *et al*., 1995; Sorensen *et al*., 1995; Ouvrard *et al*., 2000; Bourgoin, Campbell, 2002; Yang, 2002; Schaefer, 2003; Grimaldi, Engel, 2005; Brożek, 2007; Wappler *et al*., 2007; Xie *et al*., 2008). Currently, these insects are assigned to their own suborder – Coleorrhyncha Myers et China, 1929 – within the Hemiptera.

Palaeontological interpretations of the relationships present a different story, as the Coleorrhyncha, being traceable back via the Progonocimicidae to the latest Permian (255 Mya), could be derived from the Cicadomorpha: Prosboloidea: Ingruidae (Popov, Shcherbakov, 1991, 1996; Shcherbakov, Popov, 2002). This lineage evolved in parallel to the true bugs – Heteroptera, acquiring some superficial similarities but retaining basic differences (Popov, Shcherbakov 1991, 1996; Shcherbakov, Popov, 2002). The Heteroptera, appearing much later in the Middle Triassic (Grimaldi, Engel, 2005; Shcherbakov, 2010), share the costal fracture and forewing-thoracic coupling device with (and doubtless descended from) a superfamily of the basal Cicadomorpha, the Scytinopteroidea, which, like the Coleorrhyncha, is derivable from the Ingruidae (Shcherbakov, 1996, 2000).

PELORIDIIDAE – THE ONLY RECENT COLEORRHYNCHA

The only extant family of the Coleorrhyncha – the Peloridiidae Breddin, 1897 comprises 17 genera and 36 described species (Evans, 1982; Popov, Shcherbakov, 1996; Burckhardt, 2009; Burckhardt *et al*., 2011). These 'moss-bugs' are minute (2.0–5.5 mm in length), cryptically coloured insects, living in wet moss in temperate and subantarctic rain forests of the Southern Hemisphere, and are considered relics of a comparatively rich fauna from past geological periods. The distribution of the Peloridiidae is restricted to New Caledonia, New Zealand, southeastern Australia and southern South America (Evans, 1982; Popov, Shcherbakov, 1991, 1996; Burckhardt, 2009; Burckhardt *et al*., 2011). Apart from the South American *Peloridium hammoniorum* Breddin, 1897 which has winged and wingless morphs, all known recent moss-bugs lack hind wings and are unable to fly. The Peloridiidae are often cited in the biogeographical literature, along with *Nothofagus* Blume, 1851, as a typical Gondwana element illustrating both dispersal and vicariance scenarios (Darlington, 1965; Gressitt, 1974; Austin *et al*., 2004), however these statements were criticized (Eskov, 1984, 1987; Eskov, Golovatch, 1996), arguing that recent transoceanic disjunctive distributions of various taxa (including far-southern ones) are merely remnants of a transpolar distribution in the geological past. However, this "ousted relicts" hypothesis could not be applied to the Peloridiidae itself, as they probably never existed in the Northern Hemisphere, even if it is applicable to Coleorrhyncha as a whole (Eskov, 1987, 1992; Popov, Shcherbakov, 1996). The Peloridiidae seems to be connected with *Nothofagus* forests. The history of this tree is rather well documented by fossil pollen, leaves, and wood (Romero, 1986; Tanai, 1986). Its biogeography was recently analysed by Swenson *et al*. (2001a, b), Cook and Crisp (2005), M. Heads (2006) and Moreira-Muñoz (2011). Extant Peloridiidae are usually found in damp moss, often on decaying mossy trunks and twigs of *Nothofagus*. They occasionally feed on moss rhizoid, or even on wood-destroying fungi or on lichens (Popov, Shcherbakov, 1996); however Cobben (1978) suggested that they may feed on wooden stems or roots.

EXTINCT COLEORRHYNCHA

Extinct Coleorrhyncha are represented by the families Progonocimicidae and Karabasiidae (Popov, Shcherbakov, 1991). The Karabasiidae (Lower Jurassic to Upper Cretaceous of Asia) are separated into two subfamilies: the blind offshoot Hoploridiinae Yu. Popov et Shcherbakov, 1991 (Lower Cretaceous of Transbaikalia), and the Karabasiinae Yu. Popov, 1985 (Lower Jurassic to Upper Cretaceous, Asia), being very probably ancestral to recent Peloridiidae (Popov, Shcherbakov, 1991, 1996; Wang *et al*., 2009; Szwedo *et al*., 2011). The second family, Karabasiidae, considered being a transitional group between the Progonocimicidae and the Peloridiidae, was reported from the Lower Jurassic to the Upper Cretaceous of Asia (Popov, Shcherbakov, 1991, 1996).

The more ancient family Progonocimicidae (Upper Permian to Upper Cretaceous, probably worldwide) comprises two subfamilies. It is definitely not a monophylum, but rather a paraphyletic assemblage (Popov, Shcherbakov, 1996; Bechly, Szwedo, 2007; Wang *et al*., 2009; Szwedo *et al*., 2011). The Progonocimicidae comprises two subfamilies, the paraphyletic Progonocimicinae Handlirsch, 1906 and the monophyletic Cicadocorinae Becker-Migdisova, 1958. The Progonocimicinae are currently considered to have been derived from the Ingruidae (Cicadomorpha: Prosboloidea) in the latest Permian. The family is known as far back as the Tatarian (?Capitanian–Changhsingian of ICS) of Permian deposits of Belmont in Australia (~Changhsingian; Tillyard, 1926) and of Isady, Ural Mts., an undescribed find

(~Capitanian; Shcherbakov, 2000). The Progonocimicidae shares some characters with early Cicadomorpha (Popov, Shcherbakov, 1991) and the family was widely spread in Eurasia, Australia and South America from the Upper Permian to the Lower Cretaceous (Handlirsch, 1906; Tillyard, 1926; Evans, 1956, 1961, 1963, 1971; Becker-Migdisova 1962a; Wootton, 1963; Popov, Wootton, 1977; Popov, 1985, 1986, 1988, 1989; Jarzembowski, 1991; Popov, Shcherbakov, 1991; Klimaszewski, Popov, 1993; Hong, 1993; Popov *et al.*, 1994; Martins-Neto *et al.*, 2003; Bechly, Szwedo, 2007; S.W. Heads, 2008; Wang *et al*. 2009, 2011; Szwedo *et al.*, 2011). The Progonocimicinae were very abundant and diverse in the Triassic, and became rare and present only in Eurasia during the Jurassic. The Permian *Actinoscytina* Tillyard, 1926 from Australia, and some Triassic genera share structural similarities with their potential 'ancestors', the Ingruidae (Popov, Shcherbakov, 1996). Other Triassic forms show considerably modified head structure and venation patterns; these probably merit separation at suprageneric level. The Triassic genus *Pelorisca* Popov et Shcherbakov, 1991 from the Ladinian–Carnian of Madygen Formation, Kyrghyzstan, fits as a hypothetical transitional form between the Progonocimicidae and the Karabasiidae. Very probably it also merits separation at the suprageneric level. This opinion needs confirmation by some still unknown body structures of this genus (Popov, Shcherbakov, 1991). The Coleorrhyncha evolved in parallel to true bugs − Heteroptera, acquiring some superficial similarities but retaining basic differences (Popov, Shcherbakov, 1991, 1996; Shcherbakov, Popov, 2002). The supposed relationships of Coleorrhyncha subunits are summarized by Szwedo *et al*. (2011).

THE COLEORRHYNCHA OF EUROPEAN DEPOSITS – A REVIEW

The first report on Coleorrhyncha from European deposits comes from Handlirsch's (1906–1908) monumental handbook. He described the genus *Progonocimex* Handlirsch, 1906 with a single species *Progonocimex jurassicus* Handlirsch, 1906 placed in his newly established family Progonocimicidae Handlirsch, 1906 (Figs 2C, 4C). The second family described there was Eocimicidae Handlirsch, 1906, with the genus *Eocimex* Handlirsch, 1906, containing only *Eocimex liassinus* Handlirsch, 1906. Both families were originally placed in the Heteroptera, and the specimens on the basis of which the descriptions were made came from Dobbertin in Mecklenburg, Germany (Fig. 1).

Later, Handlirsch (1939) described the genera *Archicercopis* Handlirsch, 1939 with *Archicercopis falcata* Handlirch, 1939, *Eocercopis* Handlirsch, 1939 with *Eocercopis ancyloptera* Handlirsch, 1939, *Cercoprisca* Handlirsch, 1939 with *Cercoprisca similis* Handlirsch, 1939 and *Cercopinus* Handlirsch, 1939 with *Cercopinus ovalis* Handlirsch, 1939, and placed them all in the family Procercopidae Handlirsch, 1906 of the 'Homoptera' (recently the family was placed in the Hemiptera: Cicadomorpha: Cercopoidea). All these specimens also came from the deposits at Dobbertin in Mecklenburg, Germany. Evans (1956) transferred all these taxa to his family Archescytinidae Evans, 1956, which he provisionally placed in the Heteroptera.

It was Becker-Migdisova (1958) who first correctly associated the Jurassic genera *Archicercopis* Handlirsch, *Eocercopis* Handlirsch, and *Cercoprisca* Handlirsch with the Coleorrhyncha, placed them in her family Cicadocoridae Becker-Migdisova, 1958 and synonymized *Cercopina* Handlirsch under *Cercoprisca* Handlirsch.

In the "Fundamentals of Palaeontology" (edited by Rohdendorf, 1962) the families Progonocimicidae and Eocimicidae were placed in the Heteroptera (Becker-Migdisova, 1962b), while the Actinoscytinidae (with Cicadocoridae synonymized under them) were placed in the Heteroptera *incertae sedis* section. Becker-Migdisova (1962b), commenting on the Coleorrhyncha, stated that the Actinoscytinidae (= Cicadocoridae) are probably ancestral to the Heteroptera.

Metcalf and Wade (1966) in their catalogue listed the genera *Archicercopis* Handlirsch, *Eocercopis* Handlirsch, *Cercopinus* Handlirsch, and *Cercoprisca* Handlirsch in the family Procercopidae, without reference to the works of Evans (1956) and Becker-Migdisova (1958, 1962b).

In their revision of some Liassic bugs from Mecklenburg, Popov and Wootton (1977), placed the Progonocimicidae in the infraorder Actinoscytinomorpha Popov, 1971 (= Triassocoridomorpha Popov, 1968) within the suborder Heteroptera of the Hemiptera order. They also synonymized Eocimicidae Handlirsch and Cicadocoridae Becker-Migdisova under Progonocimicidae. Further, the genus *Eocimex* Handlirsch was synonymized under *Progonocimex* Handlirsch, and therefore the latter compres two species *P. jurassicus* Handlirsch, and *P. liassinus* (Handlirsch). Similarly, the genus *Cercoprisca* Handlirsch was synonymized under *Eocercopis* Handlirsch, resulting in two species comprised there, *i.e*. *E. ancyloptera* Handlirsch (Fig. 2F), and *E. similis* (Handlirsch) (Fig. 2G); the genus *Archicercopis* Handlirach remained monotypic, with *A. falcata* Handlirsch (Fig. 2D).

The Coleorrhyncha from the Jurassic deposits of Europe were later discussed by Popov and Shcherbakov (1991). In this paper the Progonocimicidae were subdivided into the Progonocimicinae and the Cicadocorinae, with additional comments and taxonomic decisions, *i.e*. synonymization of *Cercopinus ovalis* Handlirsch, 1939 under *Eocercopis*, resulting in *E. ovalis* (Handlirsch), as the third species of this genus (Fig. 2H). In addition *Progonocimex liassinus*

Fig. 1. Toarcian palaeogeography of Northwestern and Central Europe with fossil localities bearing Coleorrhyncha indicated

Note that Forthampton fossil site (marked with white) is of the latest Triassic age (after Ansorge, 2003, modified); landmasses marked with dark grey

(Handlirsch) was synonymized under *P. jurassicus* Handlirsch (Fig. 2C).

Carpenter (1992) in the volumes of the "Treatise on Invertebrate Paleontology" concerning insects, treated the Progonocimicidae as a family of the Heteroptera, following the generic synonymy of Popov and Wootton (1977), with *Cercopinus* Handlirsch synonymized under *Eocercopis* Handlirsch in addition. It must be noted that Carpenter finished the work on the "Treatise..." in 1985, *i.e.* before the paper of Popov and Shcherbakov (1991) had become available.

Additional data were presented by Popov *et al*. (1994) concerning the presence of the Progonocimicidae in the Upper Triassic of England, and of undescribed forms of the family from the Liassic of Grimmen, Western Pomerania, Germany (Fig. 1). This paper presents the first data on the Uppermost Triassic representatives of this family, ascribed to the genus *Archicercopis* Handlirsch, but without specific placement (Fig. 2A). This statement was based on the specimen formerly mentioned and figured by Brodie (1845) as "Homopterous insect" (Fig. 2B), represented by the specimen from Forthampton (labeled 'Hasfield'), Gloucestershire, UK, and which comes from the Uppermost Triassic, *Pseudomonotis* beds.

It must be noted that Progonocimicidae have been reported also from the Lower Cretaceous deposits of England. These records comprise *Yuripopovia* Jarzembowski, 1991 with *Y. woottoni* Jarzembowski, 1991 and *Y. vectense* Heads, 2008 (Jarzembowski, 1991; Heads, 2008), *Ildavia shcherbakovi* Yu. Popov, 1993 and *Valdiscytina jarzembowskii* Yu. Popov, 1993 (Klimaszewski, Popov, 1993).

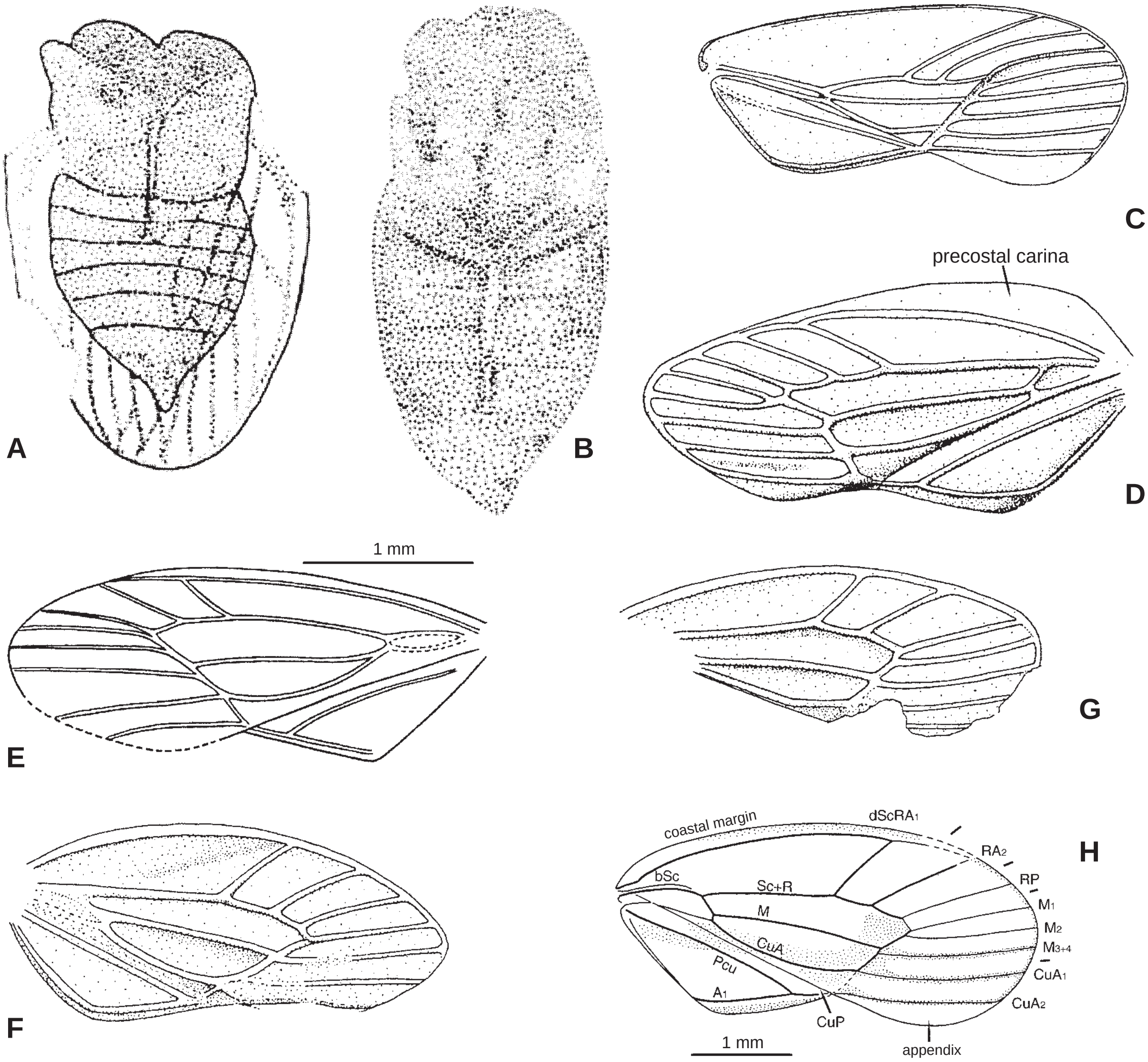

Fig. 2. Coleorrhyncha from European deposits

A. *Archicercopis* sp., uppermost Triassic of England. **B.** “Homopterous insect” of Brodie (1845), uppermost Triassic of England. **C.** *Progonocimex jurassicus* Handlirsch, left tegmen. **D.** *Archicercopis falcata* Handlirsch, Lower Toarcian of Germany. **E.** *Mesocimex anglicus* (Yu. Popov, Dolling et Whalley, 1994), Lower Toarcian of England. **F.** *Eocercopis ancyloptera* Handlirsch, Lower Toarcian of Germany. **G.** *Eocercopis similis* (Handlirsch), Lower Toarcian of Germany. **H.** *Eocercopis ovalis* (Handlirsch), Lower Toarcian of Germany. Figures A, B and E after Popov *et al.* (1994), modified; C, D, F and G after Popov and Wootton (1977), modified; H after Popov, Shcherbakov (1991), modified

A new Early Jurassic genus is described below, and in addition rich material from Grimmen (Western Pommerania, Germany), previously mentioned by Popov *et al*. (1994) and Ansorge (2003), is also under investigation. Coleorrhyncha of the superfamily Progonocimicidae were also mentioned by Ansorge (2003) from other localities in Germany: Schandelah (Lower Saxony) and Mistelgau (near Bayreuth, Upper Franconia). What is interesting is that, the proportion of these insects in particular localities is different: 10% in Grimmen, 4% in Dobbertin, 1.7% in Mistelgau and only 0.7% in Schandelah (Ansorge, 2003).

The European material listed here has brought the record of Coleorrhyncha from the uppermost Triassic to the Lower Cretaceous. The subfamily Progonocimicinae is represented by *Progonocimex* Handlirsch, 1906, with type species *Progonocimex jurassicus* Handlirsch, 1906: p. 494, from the

Lower Jurassic (Upper Lias); Dobbertin, Germany (= *Eocimex* Handlirsch, 1906, type species: *E. liassinus* Handlirsch, 1906: p. 494, from the same locality). In addition, Ansorge (2003) figured a wingless female (p. 299, fig. 3B) and tegmen (p. 299, fig. 3C), both ascribed to the genus *Progonocimex* from the Lower Jurassic of Grimmen, Western Pomerania, Germany. The new genus and species *Indutionomarus treveriorum* gen. et sp. nov. is described below.

The record of the subfamily Cicadocorinae is richer. Its oldest members are from the uppermost Triassic deposits of England, *i.e*. *Archicercopis* sp., and the Jurassic type species of the genus, *i.e. Archicercopis falcata* Handlirsch, 1939: p. 142, from the Lower Toarcian of Dobbertin, Mecklenburg, Germany. The other Jurassic genus of this subfamily is *Eocercopis* Handlirsch, 1939, with type species *Eocercopis ancyloptera* Handlirsch, 1939: p. 143, from the Lower Toarcian of Dobbertin, Mecklenburg, Germany. The subdivision of this genus is as follow: *E. ancyloptera*, *E. ovalis* (Handlirsch, 1939) [= *Cercopinus ovalis* Handlirsch, 1939: 143] and *E. similis* (Handlirsch, 1939) [= *Cercoprisca similis* Handlirsch, 1939: p. 143], all from the same locality. The Cretaceous representatives of the Cicadocorinae are: *Ildavia* Yu. Popov, 1993 *in* Klimaszewski, Popov (1993), with type species *I. shcherbakovi* Yu. Popov (1993): p. 25, from the Late Hauterivian, Lower Weald Clay, clay interval beneath British Geological Survey sandstone 3a, Clockhouse (Butterly) Brickworks near Capel, Surrey, U.K., *Valdiscytina* Yu. Popov, 1993 *in* Klimaszewski, Popov (1993), with its type species *V. jarzembowskii* Yu. Popov, 1993: p. 27, from Late Hauterivian Lower Weald Clay, clay interval beneath British Geological Survey sandstone 3a, Keymer Brickworks near Capel, Surrey, U.K.; and *Yuripopovia* Jarzembowski, 1991, with its type species *Y. woottoni* Jarzembowski, 1991: p. 99, from the Upper Hauterivian; Lower Weald Clay, Clockhouse (Butterly) Brickworks, Surrey, U.K and *Y. vectense* Heads, 2008, from the Upper Hauterivian; Upper Shepherd's Chine Member, Vectis Formation, Wealden Group; near Atherfield, Isle of Wight, U.K.

SYSTEMATICS

MATERIAL AND METHODS

The extraordinary well preserved fossils described herein come from the previously mentioned Lower Toarcian carbonate nodules, intercalated in the bituminous shales of the Exaratum Subzone (lower Falciferum Zone) exposed in Bascharage, Grand-Duché-du-Luxembourg. The other specimens from this site, *i.e.* Blattodea, Odonata, Coleoptera, Planipennia, Diptera, Lepidoptera, Orthoptera, Phasmatodea, Mecoptera, and Hymenoptera were listed or described by Maubeuge (1973), Nel (1989), Delsate *et al*. (1992), Nel and Henrotay (1992, 1994), Nel *et al*. (1993, 2004), Henrotay *et al*. (1997, 1998), Fleck *et al*. (2003), Nel (pers. comm., 2011).

An Olympus SZH10 stereoscopic microscope equipped with a camera lucida and digital camera Olympus Camedia C-5060 was used for microscopic examination, with direct, normal and polarized light. Photographs have been taken using an Olympus Camedia C-5060 digital camera and adjusted using Combine ZP and Adobe® Photoshop Elements 6.0. SEM examination was taken using a Hitachi S-3400N Scanning Electron Microscope in Low Vacuum mode in the Laboratory of Scanning Microscopy of the Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw.

The venation terminology follows the general scheme of Kukalová-Peck (1991), with slightly modified interpretation proposed by Popov and Shcherbakov (1991).

Abbreviations

bSc – basal portion of subcosta
dScRA$_1$ – common branch of distal portion of subcosta and first branch of radius anterior
R – radius
dSc – distal portion of subcosta
Sc+R – common stem of subcosta and radius
dSc+R – common stem of distal portion of subcosta and radius
dSc+RA$_1$ – common terminal of distal portion of subcosta and first branch of radius anterior
RA$_2$ – second terminal of radius anterior (R1 according to Popov, Shcherbakov, 1991)
RP – radius posterior (RS according to Popov, Shcherbakov, 1991)
M – media
M$_{1+2}$ – common stalk of M$_1$ and M$_2$
M$_1$ – first branch of media
M$_2$ – second branch of media
M$_{3+4}$ – common terminal of third and fourth branch of media
CuA – cubitus anterior
CuA$_1$ – first branch of cubitus anterior
CuA$_2$ – second branch of cubitus anterior
CuP – cubitus posterior (costal fracture; claval fracture according to Popov, Shcherbakov, 1991)
Pcu – postcubitus
A$_1$ – first anal vein
Pcu+A$_1$ – fused stalk of postcubitus and first anal vein
r-m – veinlet between radius and media
m-cua – veinlet between median and cubitus anterior.

Institutional abbreviation

The material described in this paper belongs to the collection of Michel Henrotay, deposited in the Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France, and abbreviated MNHN.

GEOLOGICAL SETTING AND PALAEOENVIRONMENTAL BACKGROUND

A considerable number of insects were collected from the Posidonia Shale of Bascharage [49°56'20"N : 5°91'70"E] (Fig. 1), Luxembourg (Grand-Duché-du-Luxembourg), whose age is Early Toarcian, Late Early Jurassic, *ca*. 183 Ma (Henrotay *et al*., 1998). The insects come from carbonate nodules which are intercalated in bituminous paper shale, and in the ammonite zonal scheme are dated more precisely in the Exaratum Subzone (lower Falciferum Zone) of the Lower Toarcian.

The fossils described herein come from fine grained, micritic calcarous nodules or layers, which were deposited under calm water, oxygen-deficient conditions, without bioturbation of the sediment (Ansorge, 2003). The insect remains occur within marine deposits, therefore they are obviously transported as dead or living specimens from adjacent land. The palaeoenvironment reconstruction was proposed by Henrotay *et al*. (1998), but criticized by Delsate *et al*. (1999).

DESCRIPTIONS

Order **Hemiptera** Linnaeus, 1758

Suborder **Coleorrhyncha** Myers et China, 1929

Superfamily **Progonocimicoidea** Handlirsch, 1906

Family **Progonocimicidae** Handlirsch, 1906

Subfamily **Progonocimicinae** Handlirsch, 1906

Genus *Indutionomarus* gen. nov.

Type species: *Indutionomarus treveriorum* sp. nov.; here designated.

Derivation of the name: Indutionomarus – name of one of the chieftains of Treveri, half-Germanic, half-Celtic tribe fighting against Gaius Julius Caesar. Gender: masculine.

Diagnosis: The new genus differs from *Progonocimex* Handlirsch, 1906 by smaller tegmen, *ca*. 3.4 mm (tegmen of *Progonocimex* longer than 5 mm); basal cell about 4.5 times as long as wide (basal cell 8 times as long as wide in *Progonocimex*); common portion of M_{1+2} present apicad of *r-m* veinlet (veinlet *r-m* connecting RP and M_1, distad of branches M_1 and M_2 separation in *Progonocimex*); base of branch M_{3+4}, veinlet *m-cua* and base of branch CuA_2 do not form a single line (oblique line formed by veinlet *r-m*, base of M_1, base of M_{3+4}, *m-cua* and base of CuA_2 in *Progonocimex*); fused veins $Pcu+A_1$ on clavus form a distinct but short common stalk (veins $Pcu+A_1$ fused almost at claval apex in *Progonocimex*).

Description. — Tegmen with rounded tip, apex of clavus reaching almost to half of total tegmen length; postclaval portion of tegmen widened. Basal cell closed apically by transverse vein. stem Sc+R forked slightly apical of stem CuA fork, stem M forked apicad of stems Sc+R and CuA forkings. Costal cell wide, slightly wider than radial cell. Venation distinctly convex, carina-like. Branch $dScRA_1$ convex at base then concave, single branch RA_2 reaching tegmen margin slightly basad of anteroapical angle; base of RP shifted mediad, terminal RP distinctly shorter than terminal M_{3+4}. Common stem of M_{1+2} dissected by veinlet *r-m*, forked well distad of *r-m* veinlet; terminal M_2 reaching apex of tegmen; terminal M_{3+4} single, almost straight, reaching apical margin mediad of tegmen apex; Branch CuA distinctly curved at base; terminal CuA_1 slightly curved mediad in apical portion; terminal CuA_2 parallel to appendix margin, reaching tegmen margin at posteroapical angle. Vein CuP forming distinct claval suture. Clavus with claval vein Pcu subparallel to claval suture, merely shifted mediad before junction with A_1; vein A_1 longer than half of claval suture length; common stem $Pcu+A_1$ about 0.23 of clavus length. Veinlet *r-m* thick as longitudinal veins, oblique, reaching common stem M_{1+2} at about half of its length; veinlet *m-cua* thick, oblique, placed in apical half of distance between stems M and CuA forkings.

***Indutionomarus treveriorum* sp. nov.**

(Figs 4A, B, 5–7)

Type material: MNHN.F.A40893* (BTDK 230a) and *MNHN.F.A40894 (BTDK 230b), print and counterprint.

Type locality: Bascharage, Grand-Duché-du-Luxembourg (Henrotay *et al*., 1998); Fig. 1.

Type horizon: Lower Toarcian, Lower Jurassic.

Derivation of the name: Specific epithet after Treveri, half-Germanic, half-Celtic tribe fighting against Gaius Julius Caesar.

Diagnosis: As for genus as it is the only included species. Additionally terminals $dScRA_1$ and RA_2 of similar length, shorter than terminal RP, terminal M_1 shorter than terminals RP and M_2; distance between separations of $dScRA_1$ and RA_2 shorter than terminal RP.

Description. — Tegmen total length 3.39 mm, maximum width 1.39 mm. Basal cell about 0.8 mm long, 0.18 mm wide. Stem Sc+R apicad of basal cell about 0.9 mm long, distance between separation of $dScRA_1$ and RA_2 0.56 mm; terminal $dScRA_1$ 0.39 mm long; terminal RA_2 about 0.54 mm long; terminal RP about 0.87 mm long. Stem M 1.08 mm long, branch M_{1+2} 0.74 mm long, terminal M_1 0.6 mm long, terminal M_2 0.64 mm long; terminal M_{3+4} 1.28 mm long. Stem CuA 0.76 mm long, terminals CuA_1 and CuA_2 1.1 mm long respectively. Total length of clavus 1.46 mm; vein Pcu before junction 1.1 mm long, vein A_1 before junction 0.76 mm long, common portion $Pcu+A_1$ 0.37 mm long. Apical cells median and cubital subequal, longer than prenodal median cell.

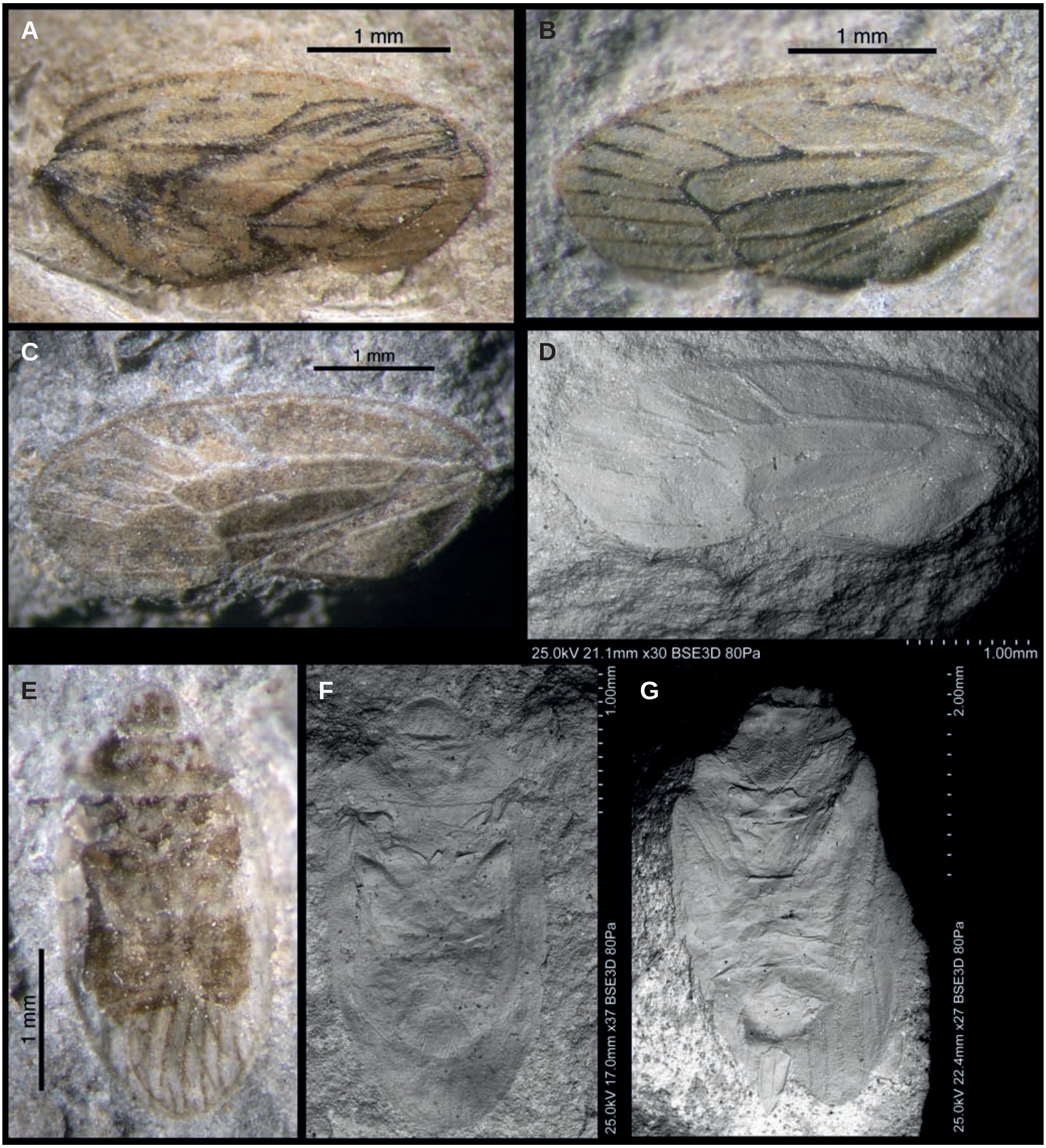

Fig. 3. A. Progonocimicinae, specimen LGA1047/1 (part), Grimmen. B. Progonocimicinae, specimen LGA1047/2 (counterpart), Grimmen. C. Cicadocorinae, specimen LGA286/1, Grimmen. D. SEM image of the same specimen. E. Cicadocorinae, LGA1027, Grimmen. F. SEM image of the same specimen. G. SEM image of the female specimen LGA1030, Grimmen, note the ovipositor structure

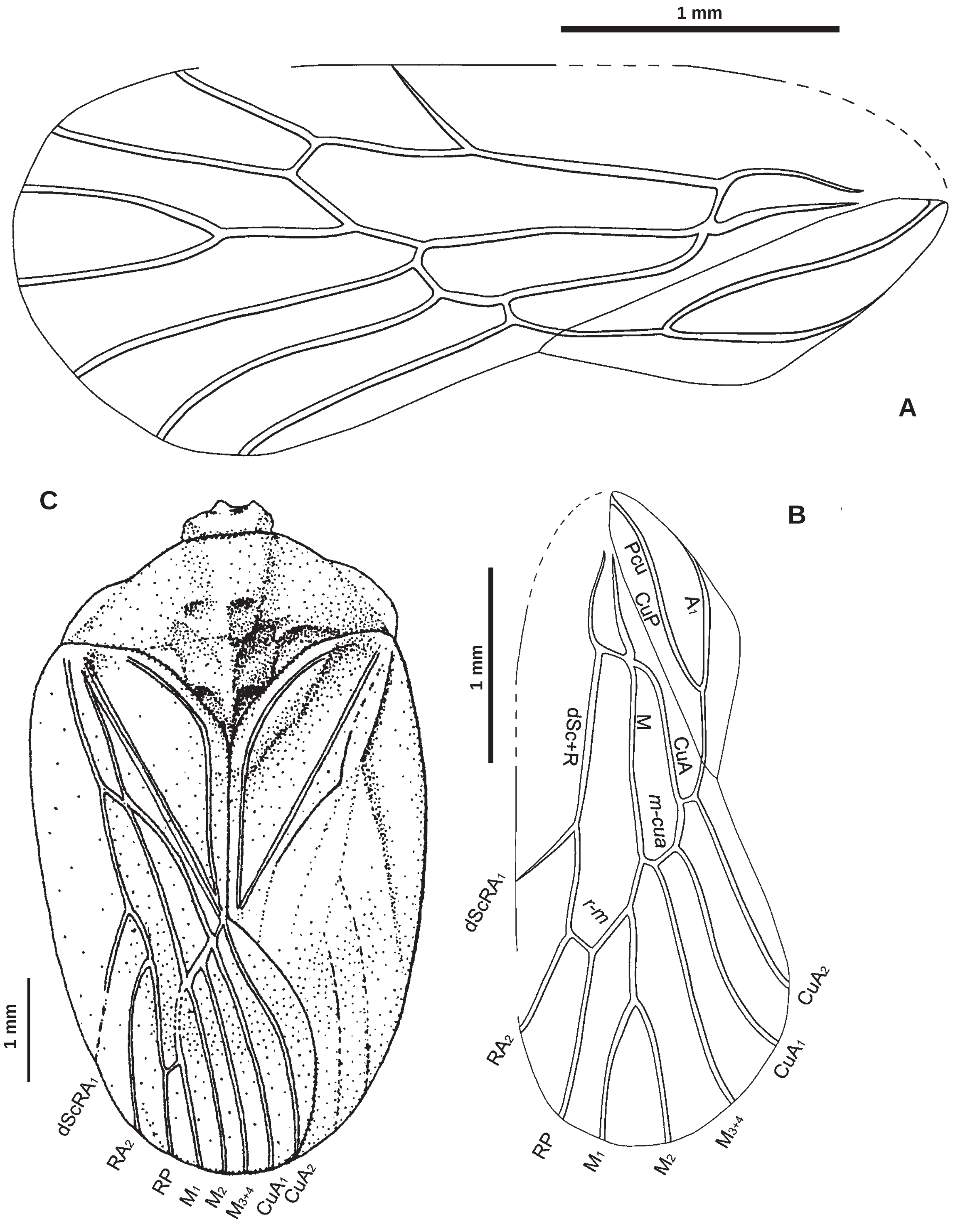

Fig. 4. A. *Indutionomarus treveriorum* gen. et sp. nov. Left tegmen (partly reconstructed). B. *Indutionomarus treveriorum* gen. et sp. nov. – venation pattern. C. *Progonocimex jurassicus* Handlirsch, 1906 (after Popov and Wootton, 1977; veins nomenclature changed); scale bars 1 mm

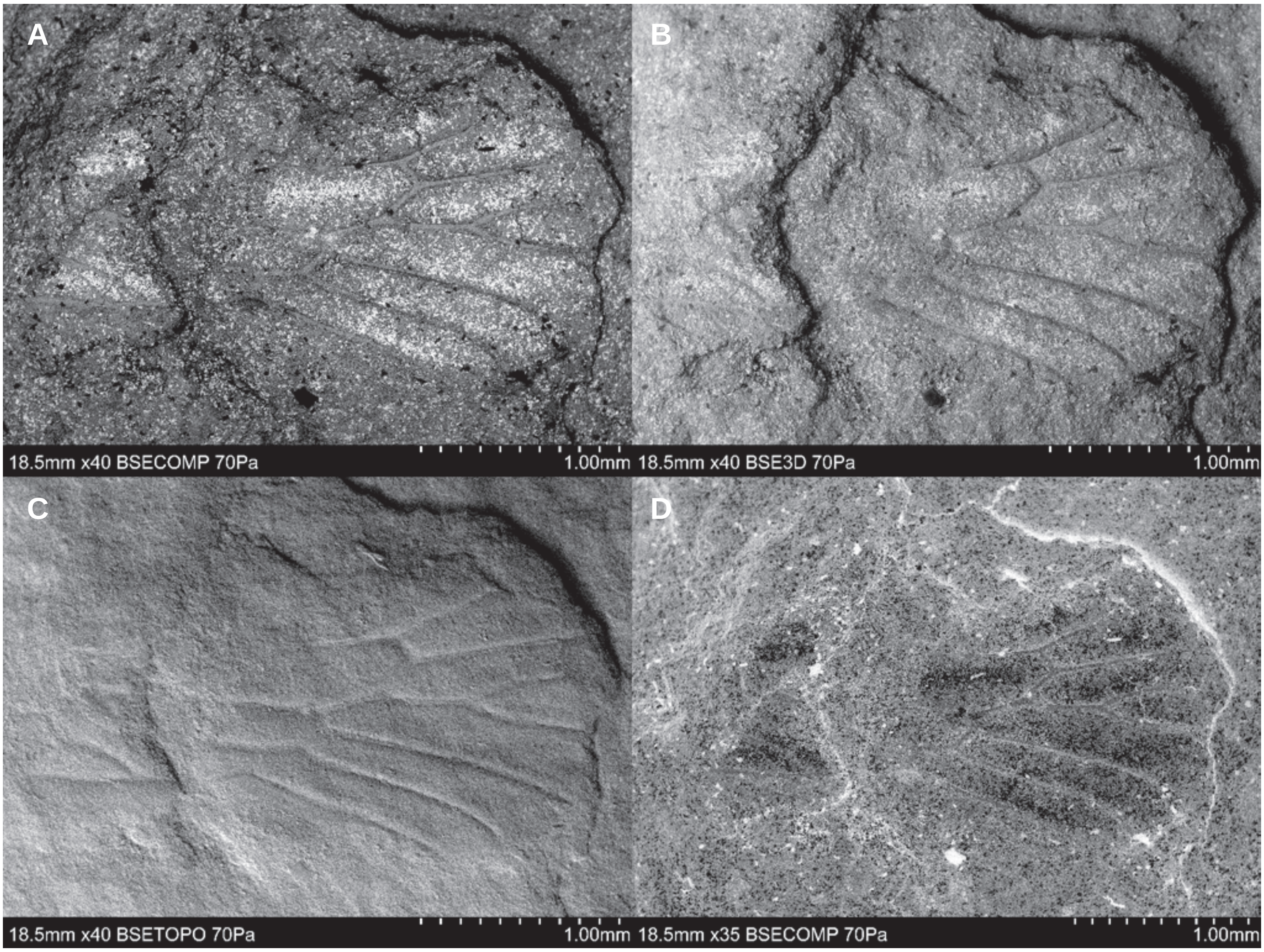

Fig. 5. ***Indutionomarus treveriorum*** **gen. et sp. nov. SEM images of print MNHN.F.A40893* (BTDK230a)**

A. Composed image mode 1. **B.** 3D mode. **C.** Topographic mode. **D.** Composed image mode 2

REMARKS

The newly established genus *Indutionomarus* gen. nov. is placed in the subfamily Progonocimicinae based on the following characters: vein A_1 not shorter than half of claval fracture, Pcu nearest to the fracture before joining A_1, dSc at least partly concave. It clearly differs from *Progonocimex* Handlirsch, 1906, by its smaller size and venation pattern.

Indutionomarus gen. nov. resembles superficially also the cicadocorine genus *Eocercopis* Handlirsch, 1939 from the Lower Toarcian of Dobbertin in Mecklenburg, Germany, but is smaller. However it shares with *Eocercopis* a relatively wide costal cell (tending to narrowing in more advanced Cicadocorinae from the Jurassic, *i.e.* some species of *Cicadocoris* Becker-Migdisova, 1958 and *Mesocimex* Hong, 1983). On the other hand, the length of the vein claval A_1 exceeding half of the length of the claval suture (vein A_1 shorter than half of claval suture in Cicadocorinae), the presence of an oblique veinlet *r-m* (straight and perpendicular in *Cicadocoris* and *Mesocimex*), and the absence of a composite transverse (more or less oblique) line separates it from the Cicadocorinae.

The Progonocimicidae were postulated not to be a monophyletic unit, but rather a paraphyletic assemblage of the stem-group Coleorrhyncha (Popov, Shcherbakov, 1996; Bechly, Szwedo, 2007; Wang *et al*., 2009; Szwedo *et al*., 2011) leading to the lineages of the Karabasiidae (Middle Jurassic – Upper Cretaceous) comprising *Karabasia* and *Hoploridium*, and the Peloridiidae (Recent). Therefore *Indutionomarus* gen. nov. could be a “transitional form” between the Progonocimicinae and the Cicadocorinae, presenting mixture of features placing it in the Progonocimicinae according to the definition of the subfamily (Popov, Shcherbakov, 1991), but sharing some

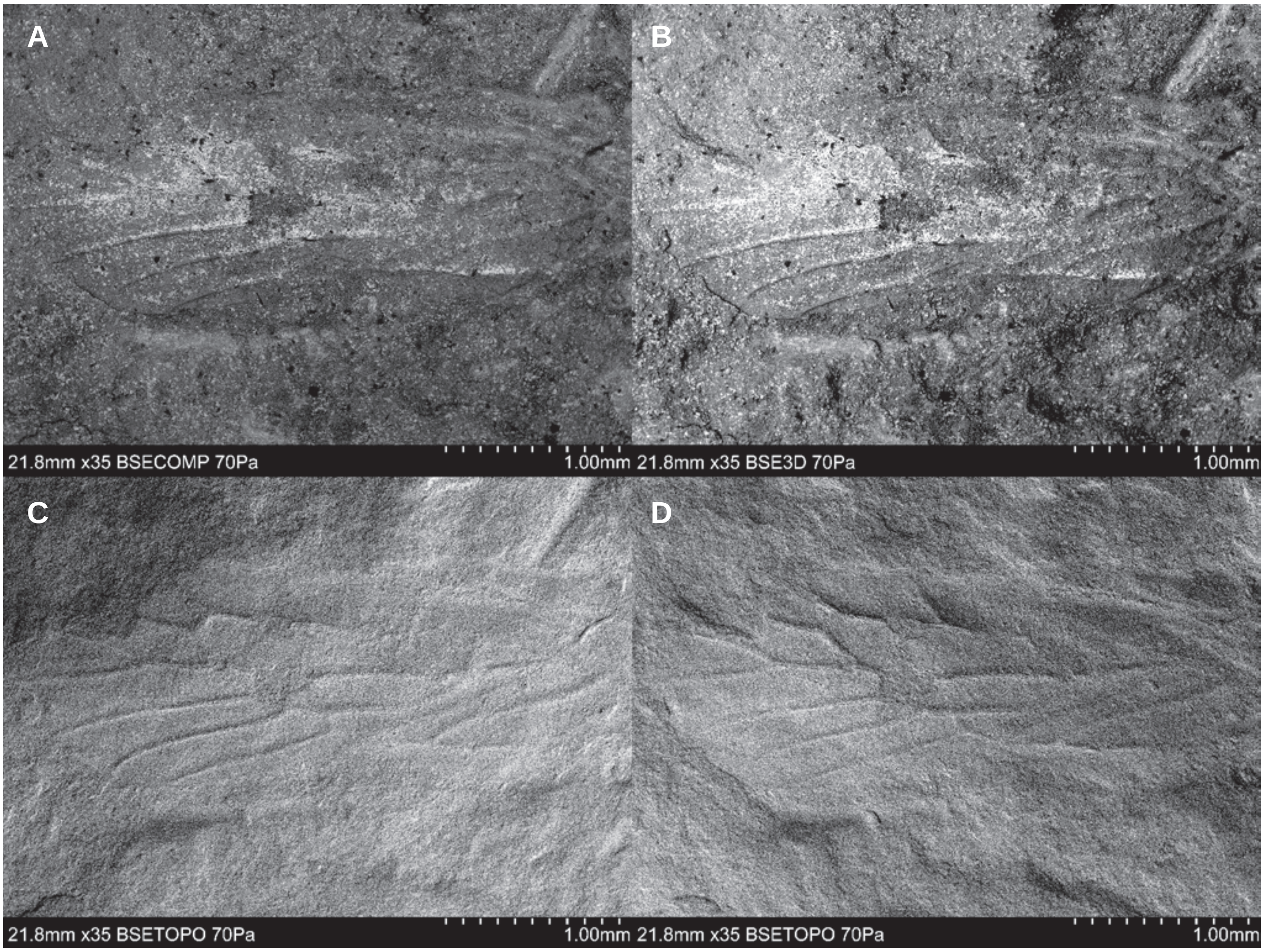

Fig. 6. ***Indutionomarus treveriorum*** **gen. et sp. nov. SEM images of counterprint *MNHN.F.A40894 (BTDK 230b)**

A. Composed image mode 1. **B.** 3D mode. **C.** Topographic mode 1. **D.** Topographic mode 2

features with their more derived relatives, features present in the Cicadocorinae. This new finding of Progonocimicidae in the European Jurassic gives a new opportunity to trace evolutionary changes in this lineage and insight to the phylogeny and relationships of the Coleorrhyncha.

NEW COMBINATION FOR MESOSCYTINA ANGLICA YU. POPOV, DOLLING ET WHALLEY, 1994

Mesocimex Hong, 1983, p. 65.

Type species: *Mesocimex sinensis* Hong, 1983, p. 65.

1958 *Olgamartynovia* Becker-Migdisova, p. 62 (type species: *Olgamartynovia turanica* Becker-Migdisova, 1958, p. 62); pro parte.

1982 *Olgamartynovia* Becker-Migdisova: Popov, p. 83.

1983 *Mesoscytina* Hong, p. 66 (type species: *Mesoscytina brunneus* Hong, 1983, p. 66) non 1919 *Mesoscytina* Tillyard, p. 871 (type species: *Mesoscytina australis* Tillyard, 1919).

1985 *Asianisca* Yu. Popov, p. 32 (type species: *Asianisca modesta* Yu. Popov, 1985, p. 33).

1991 *Mesoscytina* Hong, 1983: Popov, Shcherbakov, p. 222.

Mesocimex anglicus (Yu. Popov, Dolling et Whalley, 1994) comb. nov.

1994 *Mesoscytina anglica* Yu. Popov, Dolling et Whalley, p. 320, fig. 4.

Popov *et al*. (1994) described a new species placed in the genus *Mesoscytina* Hong, 1983, *i.e. Mesoscytina anglica* Yu. Popov, Dolling et Whalley, 1994. This taxon is based

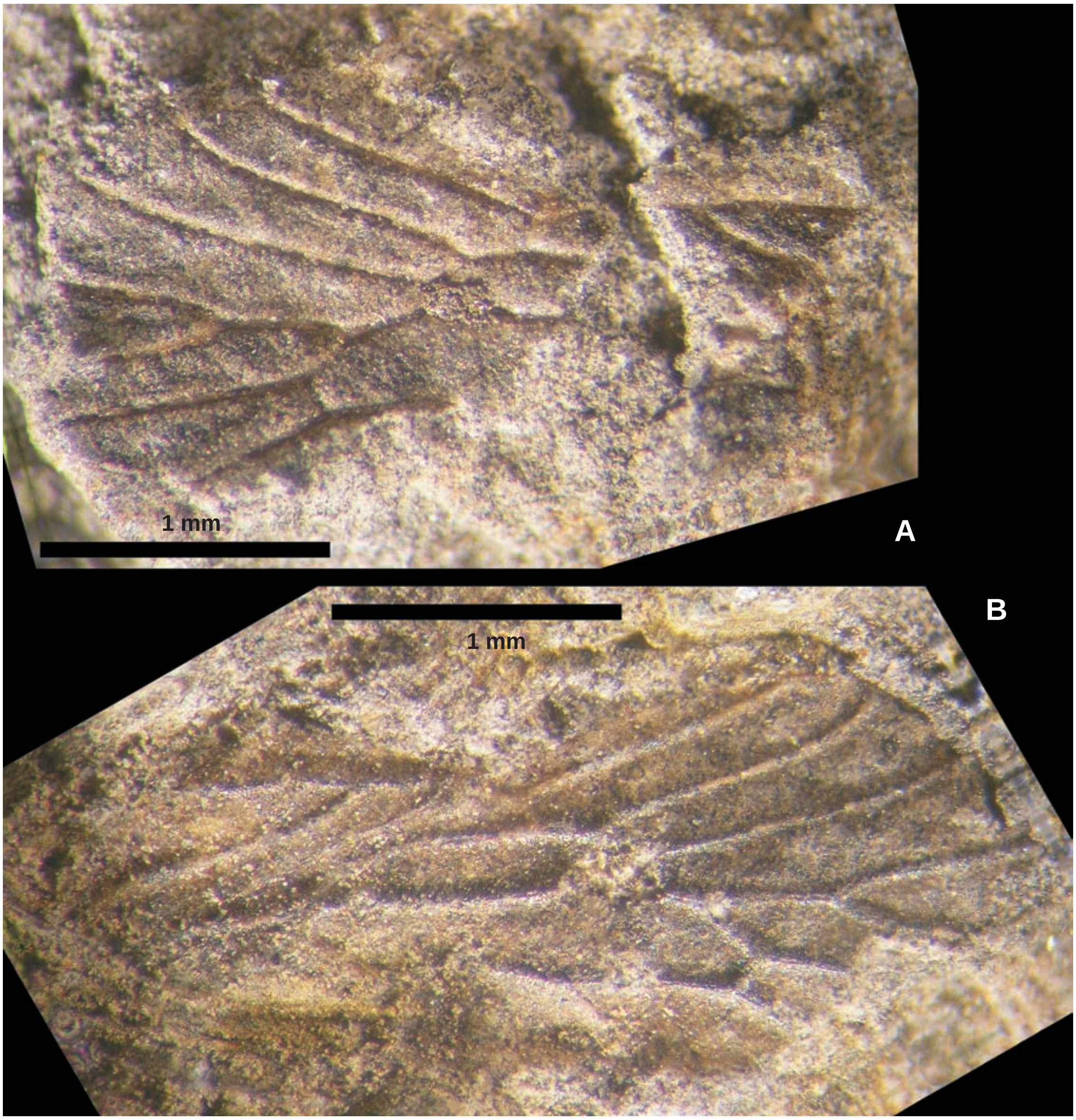

Fig. 7. ***Indutionomarus treveriorum*** **gen. et sp. nov. Light microscope images**

A. Print MNHN.F.A40893* (BTDK230a). B. Counterprint *MNHN.F.A40894 (BTDK230b); Scale bars 1 mm

on a specimen originating from the Brodie collection, from Morton Bagot, Warwickshire, England, which comes from the Lower Lias. Unfortunately, the generic name *Mesoscytina* had already been used for a genus of the Scytinopteridae (Hemiptera: Cicadomorpha). The nomenclatorial issues involved in this name and the availability of synonymic names were discussed by Wang *et al*. (2009), but *Mesoscytina anglica* was missed by these authors. According to the synonymy proposed by Wang *et al.* (2009), this species should be placed in the genus *Mesocimex* Hong, 1983 as *Mesocimex anglicus* (Yu. Popov, Dolling et Whalley, 1994) comb. nov. (Fig. 2E). The species of the genus *Mesocimex* are recorded from the Lower–Middle Jurassic of Central and East Asia, so this record from England is its westernmost occurrence.

THE IMPORTANCE OF PROGONOCIMICIDAE FROM THE EUROPEAN JURASSIC

All the representatives of the Jurassic Progonocimicidae in Western and Central Europe deposits comes from a short period of about 600.000 years restricted to the Toarcian Oceanic Anoxic Event (T-OAE), spanning upper Tenuicostatum Zone and lower Falciferum Zone (Exaratum Subzone). The T-OAE was the period of profound environmental changes, coeval with carbon cycle perturbations, elevated carbon dioxide content, global warming and humidification (Jenkyns, 1988; Wignall *et al*., 2005; Hesselbo *et al*., 2000, 2007; Suan *et al*., 2008; Gómez *et al*., 2008; Hesselbo, Pieńkowski, 2011; Dera *et al*., 2011). In general, the composition of the Early and Middle Jurassic floras of the Euro-Sinian region were mainly composed of horsetails, ferns, seed ferns, cycads, bennettitaleans, cycadophytes, ginkgos and conifers (Vakhrameev, 1988, 1991). An extremely warm and humid climate at that time is reflected in the changes in floral composition and vegetation, with local dominance of hygrophilous plants, such as moss (Bryophyta), club-mosses (Lycopsida), quill worts (Isoetaceae), ferns and others (Hesselbo, Pieńkowski, 2011). The presence of the xerophythic (drought-resistant) and thermophythic Cheirolepidaceae is considered to reflect warm but more arid conditions (Vakhrameev, 1982, 1988, 1991; de Oliveira *et al*., 2008; Barrón *et al*., 2010). A humid belt would have existed along the Toarcian shore lines, while coniferous, more xerophytic vegetation scrub of Cheirolepidiaceae and other gymnosperms such as Araucariaceae, Taxodiaceae, Gingkoales and sellaginellous cryptogams, and ferns adapted to the dry environments in the undergrowth of these taxa, would probably have dominated the landscape in the drier interiors of European landmasses (Vakhrameev, 1988, 1991; Barrón *et al*., 2010). Wade-Murphy *et al*. (2006) showed evidence for significant changes in the land plant community occurring contemporaneously with the ecological crises in the marine realm during T-OAE. They suggested that the mechanisms that were involved must have affected synchronously both the marine and continental ecosystems and favoured a primary role for large-scale volcanism in the Toarcian. According to Rees *et al*. (2000), the European insectiferous deposits were formed in the warm temperate zone.

The insect remains occur within marine deposits, therefore they are obviously redeposited from adjacent land. As the occurrences of insects in the Lower Toarcian of Middle and Western Europe (Ansorge, 2003) are restricted to this short, specific period of time, their presence could be linked to palaeoclimatic and palaeoecological conditions. The coincidence with T-OAE suggests that the Early Jurassic Progonocimicidae could be characteristic of much warmer and maybe more humid conditions. It is generally accepted that the host-plants of these extinct Coleorrhyncha should be found among the gymnosperms (Popov, Shcherbakov, 1996). Very probably nymphs were cryptic on thick stems, while imagoes were jumping on larger plants (Popov, Shcherbakov, 1996). The Early Jurassic Progonocimicidae are of great interest, particularly as the members of late Progonocimicinae found present some features characteristic of their descendants, the Cicadocorinae. The latest Triassic/Earliest Jurassic seems to be the epoch of separation of the Cicadocorinae, which dominated in the Jurassic and survived until the beginning of the Late Cretaceous. Members of this subfamily developed powerful hind legs provided with movable lateral spurs and apical teeth on their tibiae and broad membranization in front of their hind coxae which gave them great jumping capabilities. These were probably the best jumpers among the Coleorrhyncha (Popov, Shcherbakov, 1996). These evolutionary changes expressed in morphological features and biological adaptations were very probably triggered by environmental conditions, climatic, floristic and vegetational. The Progonocimicidae from Europe and Central and East Asia are very similar in the wing venation and body structures. That is why much taxonomic confusion exists in the Jurassic Progonocimicidae. The similarity suggests a strong faunal exchange within Laurasia during the Jurassic. This could be the result of the concentration of Jurassic plant productivity and maximum diversity at middle latitudes (Rees *et al*., 2000), enabling dispersal and wide range of plant-sucking insects.

The findings of Coleorrhyncha in the European Jurassic give new insights in the evolutionary scenario of the group and opportunities for better understanding of palaeoenvironmental conditions and the relationships of insects, their host-plants and palaeohabitats.

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