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 Peloridiidea 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; Pendergraft, 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
a paraphyletic assemblage (von Dohlen, Moran, 1995; Sørensen et al., 1995; Brozék 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 proven by several molecular phylogenetic studies and morphological evidence (Schlee, 1969; Wheeler et al., 1993; Campbell et al., 1995; Sørensen et al., 1995; Ouvrard et al., 2000; Bourgoin, Campbell, 2002; Yang, 2002; Schaefer, 2003; Grimaldi, Engel, 2005; Brozék, 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: Prosoboloidea: 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 Bredtin, 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 Bredtin, 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 transoceanic 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: Proso- boloidea) in the latest Permian. The family is known as far back as the Tatarian (’Capitanian–Changhsingsian of ICS) of Permian deposits of Belmont in Australia (–Changhsingsian; Tillyard, 1926) and of Isady, Ural Mts., an undescribed find
Coleorrhyncha (Insecta: Hemiptera) of the European Jurassic...

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 Dobbentin in Mecklenburg, Germany (Fig. 1).

Later, Handlirsch (1939) described the genera Archicerocipis Handlirsch, 1939 with Archicerocipis falcata Handlirsch, 1939, Eocerocipis Handlirsch, 1939, Eoceropis Handlirsch, 1939 with Eoceropis 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 Progonocimicidae Handlirsch, 1906 of the ‘Homoptera’ (recently the family was placed in the Hemiptera: Cicadomorpha: Cercopoidea). All these specimens also came from the deposits at Dobbentin in Mecklenburg, Germany. Handlirsch (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 Archicerocipis Handlirsch, Eocerocipis Handlirsch, and Cercoprisca Handlirsch with the Coleorrhyncha, placing them in her family Cicadocoridae Becker-Migdisova, 1958 and synonymized Cercopina Handlirsch under Cercoprisca Handlirsch.

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


In their revision of some Liassic bugs from Mecklenburg, Popov and Wootton (1977), placed the Progonocimicidae in the infraorder Actinoscytiformes Popov, 1971 (= Triasocoridomorpha 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 comprises two species P. jurassicus Handlirsch, and P. liassinus (Handlirsch). Similarly, the genus Cercoprisca Handlirsch was synonymized under Eocerocipis Handlirsch, resulting in two species comprised there, i.e. E. ancyloptera Handlirsch (Fig. 2F), and E. similis (Handlirsch) (Fig. 2G); the genus Archicerocipis Handlirsch 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 Progonocimicidae and the Cicadocoridae, with additional comments and taxonomic decisions, i.e. synonymization of Cercopinus ovalis Handlirsch, 1939 under Eocerocipis, resulting in E. ovalis (Handlirsch), as the third species of this genus (Fig. 2H). In addition Progonocimex liassinus...
(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.

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 (= Eoctimex 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 Progonocicimex from the Lower Jurassic of Grimmen, Western Pomerania, Germany. The new genus and species Indutionomarus treveriorm gen. et sp. nov. is described below.


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

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>bSc</td>
<td>basal portion of subcosta</td>
</tr>
<tr>
<td>dScRA1</td>
<td>common branch of distal portion of subcosta and first branch of radius anterior</td>
</tr>
<tr>
<td>R</td>
<td>radius</td>
</tr>
<tr>
<td>dSc</td>
<td>distal portion of subcosta</td>
</tr>
<tr>
<td>Sc+R</td>
<td>common stem of subcosta and radius</td>
</tr>
<tr>
<td>dSc+R</td>
<td>common stem of distal portion of subcosta and radius</td>
</tr>
<tr>
<td>dSc+RA1</td>
<td>common terminal of distal portion of subcosta and first branch of radius anterior</td>
</tr>
<tr>
<td>RA2</td>
<td>second terminal of radius anterior (R1 according to Popov, Shcherbakov, 1991)</td>
</tr>
<tr>
<td>RP</td>
<td>radius posterior (RS according to Popov, Shcherbakov, 1991)</td>
</tr>
<tr>
<td>M</td>
<td>media</td>
</tr>
<tr>
<td>M1,2</td>
<td>common stalk of M1 and M2</td>
</tr>
<tr>
<td>M1</td>
<td>first branch of media</td>
</tr>
<tr>
<td>M2</td>
<td>second branch of media</td>
</tr>
<tr>
<td>M3,4</td>
<td>common terminal of third and fourth branch of media</td>
</tr>
<tr>
<td>CuA</td>
<td>cubitus anterior</td>
</tr>
<tr>
<td>CuA1</td>
<td>first branch of cubitus anterior</td>
</tr>
<tr>
<td>CuA2</td>
<td>second branch of cubitus anterior</td>
</tr>
<tr>
<td>CuP</td>
<td>cubitus posterior (costal fracture; claval fracture according to Popov, Shcherbakov, 1991)</td>
</tr>
<tr>
<td>Pcu</td>
<td>postcubitus</td>
</tr>
<tr>
<td>A1</td>
<td>first anal vein</td>
</tr>
<tr>
<td>Pcu+A1</td>
<td>fused stalk of postcubitus and first anal vein</td>
</tr>
<tr>
<td>r-m</td>
<td>veinlet between radius and media</td>
</tr>
<tr>
<td>m-cua</td>
<td>veinlet between median and cubitus anterior</td>
</tr>
</tbody>
</table>

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 calcareous 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 M1+2 present apicad of r-m veinlet (veinlet r-m connecting RP and M1, distad of branches M1 and M2, separation in Progonocimex); base of branch M1+2, veinlet m-cua and base of branch CuA2 do not form a single line (oblique line formed by veinlet r-m, base of M1, base of M1+2, m-cua and base of CuA2 in Progonocimex); fused veins Pcu+CuA fused on clava form a distinct but short common stalk (veins Pcu+CuA1 fused almost at claval apex in Progonocimex).

Description. — Tegmen with rounded tip, apex of clava 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 dScRA1 forked well distad of r-m veinline; terminal M1, reaching apex of tegmen; terminal M1+2 single, almost straight, reaching apical margin mediad of tegmen apex; Branch CuA distinctly curved at base; terminal CuA, slightly curved mediad in apical portion; terminal CuA parallel to appendix margin, reaching tegmen margin at posteroapical angle. Vein CuP forming distinct claval suture. Clava with claval vein Pcu subparallel to claval suture, merely shifted mediad before junction with A1; vein A1 longer than half of claval suture length; common stem Pcu+CuA2 about 0.23 of clava length. Veinlet r-m thick as longitudinal veins, oblique, reaching common stem M1+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 dScRA1 and RA2 of similar length, shorter than terminal RP, terminal M1 shorter than terminals RP and M2; distance between separations of dScRA1 and RA2 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 dScRA1 and RA2 0.56 mm; terminal dScRA1 0.39 mm long; terminal RA2 about 0.54 mm long; terminal RP about 0.87 mm long. Stem M 1.08 mm long, branch M1+2 0.74 mm long, terminal M1 0.6 mm long, terminal M2 0.64 mm long; terminal M1+2 1.28 mm long. Stem CuA 0.76 mm long, terminals CuA1 and CuA2 1.1 mm long respectively. Total length of clava 1.46 mm; vein Pcu before junction 1.1 mm long, vein A1 before junction 0.76 mm long, common portion Pcu+CuA 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
The newly established genus *Indutionomarus* gen. nov. is placed in the subfamily Progonocimicinae based on the following characters: vein A₁ not shorter than half of claval fracture, Pcu nearest to the fracture before joining A₁, 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 A₁ exceeding half of the length of the claval suture (vein A₁ 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
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.


_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...
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 Falceiferum 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 gymnosperms, such as moss (Bryophyta), club-mosses (Lycopsidea), quill worts (Isoetaceae), ferns and others (Hesselbo, Pieńkowski, 2011). The presence of the xerophytic (drought-resistant) and thermophytic 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 selaginellous 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 palaeocological 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 imagos were jumping on larger plants (Popov, Shcherbakov, 1996). The Early Jurassic Progonocimicidae are of great interest, particularly as the members of late Progonocimicidae 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 membrane 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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