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First fossil record of the mayfly family Baetiscidae from Baltic amber (Insecta: Ephemeroptera)

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With 10 Figures

Abstract

A new genus and species of mayflies (Insecta: Ephemeroptera) from Baltic amber is described: *Balticobaetisca velteni* n. g., n. sp. is the first fossil record of Baetiscidae and the first Old World record for this family. The biogeographical and phylogenetic implications of this discovery and the phylogenetic position of Baetiscidae are discussed.

Zusammenfassung

Eine neue Eintagsfliegengattung und -art (Insecta: Ephemeroptera) aus dem Baltischen Bernstein wird beschrieben: *Balticobaetisca velteni* n. g. n. sp. ist der erste Fossilnachweis sowie der erste altweltliche Nachweis für die Baetiscidae. Die phylogenetischen und biogeographischen Implikationen dieses Neufundes sowie die phylogenetischen Beziehungen der Baetiscidae werden diskutiert.

1. Introduction

The Baetiscidae, also known as "armored mayflies", is a small mayfly family in which currently ten valid extant species are recognized (PESCADOR & BERNER 1981). Their Recent distribution is restricted to North America (BERNER & PESCADOR 1980), and until now this family has not been present in the fossil record at all (KEILBACH 1982, HUBBARD 1987, CARPENTER 1992, SPAHR 1992). In this paper the first fossil record for the Baetiscidae is described which is also the first Old World record for this family. The biogeographical implications of this finding are discussed. The Baetiscidae are classified together with the Prosopistomatidae as Prosopistomatoidea (EDMUNDS & TRAVER 1954a). While previous authors included the Prosopistomatoidea as a taxon within the pannote mayflies (MCCAFFERTY & EDMUNDS 1979), the Prosopistomatoidea have been recently regarded as the sistergroup of all other mayflies (KLUGE et al. 1995, MCCAFFERTY & WANG 2000). The arguments for these two contradicting hypotheses are herein discussed as well.



Fig.1. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, habitus in ventral view, photo. Scale 10 mm.



Fig.2. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, body in dorsal view (arrow marks stellate hair), photo. Without scale.

Methods

All drawings were made with a camera lucida on a Wild M5 binocular microscope, and the photos have been made with a Nikon Coolpix 995 digital camera on the same microscope with photo adapter, except for Figure 2 which was made with a Canon T70 SLR camera and photo tubus. Figure 1 was made with a Agfa SnapScan flatbed scanner by directly scanning the piece of amber. Figure 8 was processed in Adobe Photoshop 5.0 to combine two original photos with different depths of field. The anatomical terminology is based on EDMUNDS & TRAVER (1954b) and KLUGE (1994).



Fig. 3. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, left forewing from ventral side, photo. Without scale.

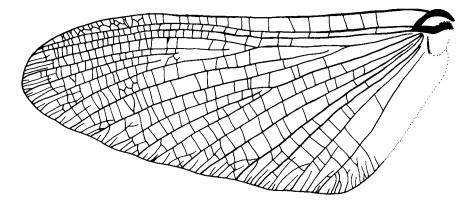


Fig. 4. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, left forewing. Scale 1 mm.



Fig. 5. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, right forewing from ventral side, photo. Without scale.

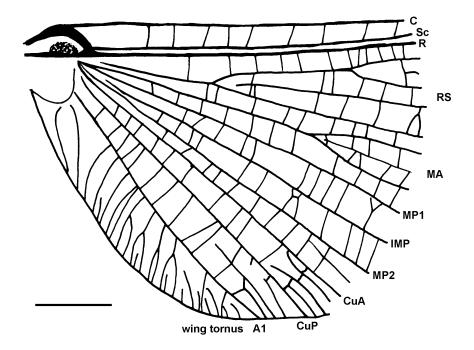


Fig.6. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, right forewing base. Scale 1 mm.



Fig.7. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, hind wing, photo. Without scale.

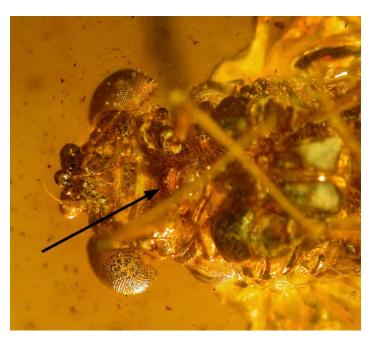


Fig.8. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, head and thorax from ventral side (arrow marks the prosternal bispinate projection), photo. Without scale.

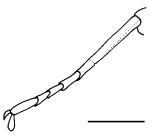


Fig.9. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, left mesotarsus. Scale 0.5 mm.

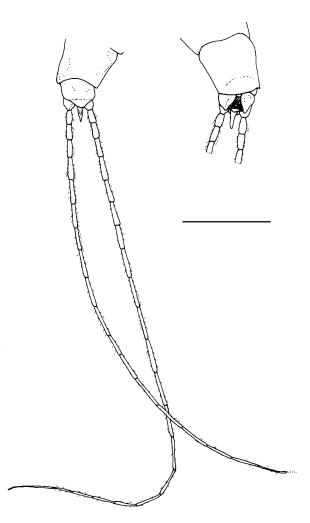


Fig.10. *Balticobaetisca velteni* n. sp., female holotype SMNS BB-2376, apical abdomen and anal appendages (left in dorsal, right in ventral view). Scale 1 mm.

2. Systematic Palaeontology

Class Insecta LINNAEUS, 1758 (= Hexapoda LATREILLE, 1825) Pterygota BRAUER, 1885 Order Ephemeroptera HYATT & ARMS, 1890 Family Baetiscidae EDMUNDS & TRAVER, 1954

Genus Balticobaetisca n. g.

Type species: Balticobaetisca velteni n. sp.

Derivation of name: Named after the type locality, the Baltic region, and the extant genus *Baetisca*.

Diagnosis. – This new fossil genus is distinguished from *Baetisca* by the following combination of characters: The lack of an apical cleft in sternum IX of the female imago; the lack of a middorsal transverse elevation in tergum VI. It is distinguished from the subgenus *Fascioculus* by eyes without vertical bands and additionally from some species of the subgenus *Baetisca* s.str. by hyaline wings. Last but not least, the fact that this fossil specimen is about 45 million years old, and lived in a geographical region that has undergone dramatic climatic changes since then, excludes any reasonable possibility that this fossil specimen might be conspecific with any other described species of *Baetisca*.

Balticobaetisca velteni n. sp. Figs. 1-10

Holotype: Female specimen no. SMNS BB-2376 in the amber collection of the Staatliches Museum für Naturkunde Stuttgart, Germany (ex coll. VELTEN).

Type locality: Baltic.

Type horizon: Eocene (40-50 mybp), Baltic amber (Succinite). This specimen has been purchased by Mr JÜRGEN VELTEN (Idstein, Germany) from a Polish trader. Its Baltic origin is confirmed by the colour and general appearance of the stone and the presence of at least one stellate hair of an oak tree (Fig. 2, arrow) which is generally regarded as a main characteristic of Baltic amber (WEITSCHAT & WICHARD 1998). Furthermore, the presence of so-called "Verlumung" (white cloudy substance) on the thorax and abdomen (Fig. 2) is a typical phenomenon of Baltic amber. Such "Verlumung" is almost unknown from Dominican amber. This clearly excludes a potential Dominican origin that might otherwise be suspected due to the exclusively Nearctic distribution of the extant representatives of Baetiscidae.

Derivation of name: Named after Mr JÜRGEN VELTEN (Idstein, Germany) who kindly donated the holotype to the amber collection of SMNS.

Diagnosis. - That of genus Balticobaetisca n. g., since monotypic.

Description. – A completely preserved female imago in Baltic amber (Fig. 1). Body length: 8.5 mm.

Head. – Frons with three prominent ocelli (Fig. 8). Eyes small, separated on meson of head by a distance twice the width of an eye.

Thorax. – Reduced prothorax. Prosternum medially with bispinate projection between forecoxae (Fig. 8, arrow). Mesoscutellum elongated. Mesosternum with medially approximated furcasternal protuberances (furcasternum contiguous without median impression).

Legs. – All claws dissimilar with one hooked and one blunt claw (Fig. 9). Tarsi each with five tarsomeres. Basitarsus merged with tibia. Meso- and metatibia with traces of a tibiopatellar suture. Length of fore leg 3.25 mm, middle leg 3.25 mm, hind leg 3 mm.

Wings. – Forewing (Figs 3-6): Length 10 mm, maximum width 4 mm. Forewing entirely hyaline, rear margin slightly scalloped. Venation in "posteritornous" condition: CuP terminates anterior of wing tornus, A1 ends apically at the outer wing margin rather than at the anal margin. RS and MA without common stem, but basally approached. MA, MP1, MP2, and CuA with common point of origin (Fig. 6). CuA and CuP basally approached, but unfused.

Hind wing (Fig. 7): Length 3.5 mm, maximum width 2.5 mm, rounded, almost circular appearance, with prominent blunt costal projection near its base and numerous long intercalaries. MA without furcation.

Abdomen (Figs 2 and 10): Robust but more elongate than in all extant Baetiscidae; tapered distally, but less so than in all extant species of Baetiscidae. Nine abdominal segments visible, segment I probably fused with metathorax and thus only tergites II-X and respectively sternites II-IX visible. Segments II-V short, of subequal length, segment VI and VII enlarged, with segment VI being the longest segment. Tergum VI without middorsal transverse elevation (Fig. 2), sternum IX without apical cleft (Fig. 10). Length of cerci 80 mm each. Paracercus very short (length 0.15 mm) and unsegmented (Fig. 10).

3. Phylogenetic considerations

Even though most synapomorphies of Prosopistomatoidea are larval characters, this fossil imago can be clearly identified as belonging to this superfamily because of the enlargement of the VIth abdominal segment and the characteristic posteritornous venation of the forewing. Furthermore, the prosternal bifid projection as well as the most characteristically rounded shape of the hind wings can be regarded as autapomorphic characters of the Baetiscidae. The entire wing venation, the dissimilar meso- and metatarsal claws, the reduced paracercus and the general habitus of the specimen leave no reasonable doubt that it belongs to the Baetiscidae. On the other hand, *Balticobaetisca velteni* n. sp. lacks some apomorphic characters that are otherwise shared by all of the extant species of *Baetisca*, namely the apical cleft in sternum IX of the female imago and the lack of a middorsal transverse elevation in tergum VI, as well as the short and chunky abdomen more tapered distally. This clearly indicates that *Balticobaetisca velteni* n. sp. is a stemgroup representative of the extant crowngroup *Baetisca*. This has been accommodated by placing *B. velteni* n. sp. into the new genus *Balticobaetisca*.

The phylogenetic relationships of the family Baetiscidae have been subject to many different hypotheses by previous authors: While VAYSSIÈRE (1934) and GILLIES (1954) soon assumed a sistergroup relationship between Baetiscidae and Prosopistomatidae on behalf of the nymphal similarities, DEMOULIN (1969) favoured a closer relationship between the Baetiscidae and Oniscigastridae. DEMOULIN supported his hypothesis mainly by the similar gill structure of these two taxa. Other shared similarities are mainly symplesiomorphies, i.e the complete wing vein triads. LANDA (1973) and LANDA & SOLDAN (1985) argued for a closer relationship between Baetiscidae and Neoephemeridae (as the sistergroup of Caenidae + Prosopistomatidae), mainly based on common fused trunks of the Malpighian tubules in both groups. EDMUNDS et al. (1976) and MCCAFFERTY & EDMUNDS (1979) proposed a sistergroup relationship between Baetiscidae and Prosopistomatidae. KLUGE et al. (1995), KLUGE (1998, 2000), and MCCAFFERTY & WANG (2000) concurred with this latter hypothesis. Indeed, the few arguments for alternative views are outweighted by the numerous striking synapomorphic characters that have been proposed for this sistergroup relationship: The notal shield with incorporated wing buds of the larva, the specific gill structure, and the fusion of all thoracic and abdominal ganglia to a thoracic synganglion.

However, there have been drastic changes in placing the Prosopistomatoidea within the Ephemeroptera: MCCAFFERTY & EDMUNDS (1979) proposed a sistergroup relationship between the Propistomatoidea and Caenoidea (Caenidae + Neoephemeridae) within the pannote mayflies (Ephemeroptera: Pannota). Based on internal anatomy, a closer relationship of these four families has also been suggested by LANDA & SOLDAN (1985). Potential synapomorphies for this monophylum could be the arrangement of the Malpighian tubules and the development of the second [sic!] pair of gills as opercula to cover the succeeding gills. The notal shield of Prosopistomatoidea has been consequently interpreted as a derived condition of the pannote medial fusion of the wing pads.

However, KLUGE et al. (1995) and KLUGE (1998, 2000) excluded the Prosopistomatoidea from the Pannota and proposed a sistergroup relationship of Prosopistomatoidea (named by him Posteritorna) with the remaining mayflies (Anteritorna). MCCAFFERTY & WANG (2000) followed this argumentation. There are only two potential synapomorphies for a monophylum Anteritorna that are mentioned by these authors, namely the anteritornous condition of the forewing and the number of dentisetae in the larval maxilla. However, the polarity of the latter character is unclear, because a detailed outgroup comparison to determine the groundplan condition in Ephemeroptera has not yet been undertaken. Concerning the wing tornus character, MCCAFFERTY & WANG (2000) maintained that the posteritornous state should be plesiomorphic, although no arguments were presented. On the other hand, KLUGE (1998, 2000) argued that both anteritornous and posteritornous condition are alternative apomorphic traits of the respective groups which evolved from a wing without tornus such as in the Permian stemgroup mayfly family Protereismatidae. Compared to these weak evidences, the putative synapomorphies for Pannota (incl. Prosopistomatoidea) seem to be more convincing and imply that the anteritornous wing condition may represent a symplesiomorphic character of Ephemeroptera.

Independently from the morphological evidence, the following argumentation casts doubt on the alleged antiquity of the clade Prosopistomatoidea that would be implied by the hypothesis of KLUGE (1998, 2000): Because Prosopistomatidae are not yet known from the fossil record, the present discovery of an Early Tertiary representative of their sistergroup Baetiscidae provides for the first time a "terminus post quem non" for the age of origin of both families. The circumstance that the new fossil genus from Baltic amber belongs to the stemgroup rather than the crowngroup of a recent family is quite extraordinary for fossil insects in Baltic amber. This suggests that the extant genus *Baetisca* might be of relatively young origin.

4. Biogeographical considerations

As mentioned above, all extant species of the Baetiscidae are distributed exclusively in North America. However, their sistergroup Prosopistomatidae is present in the Holarctic, Ethiopian, Oriental, and Australian region, while it is completely absent from America. Consequently, the present discovery of a stemgroup Baetiscidae from the Old World could be interpreted as evidence for an origin of this family outside of the Nearctic realm.

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