INTRODUCTION

The genus Baltameletus Demoulin, 1968 was established for the species B. oligocaenicus Demoulin, 1968 (Demoulin 1968: 238, Figs 3a–f). The description is based on a single specimen of a male subimago from Baltic Eocene amber (W. Simon amber collection in the Museum für Naturkunde, Institute of
Palaeontology, Humboldt University, Berlin, inventory number MB.J 2248). Georges Demoulin (1968) placed this fossil genus in the subfamily Siphlonurinae Banks, 1900 within the family Siphlonuridae Banks, 1900, and this suggestion was accepted by the majority of specialists (Tshernova 1970, Hubbard 1987, 1990). In Demoulin’s opinion, the characteristics enabling separation of the genus Baltameletus from other Siphlonurinae, are as follows: the availability of large triangular protuberance on the lateral sides of tergum IX; the structure of veins iMP and MP₂ in forewings, each of them being connected with CuA and MP being distinctly longer that MP₂ (Demoulin 1968: 238–240, Fig. 3b, e). Kluge (2004: 355) used the non-ranking hierarchical name Baltameletus/g for the genus Baltameletus and placed this taxon within Anteritorna incertae sedis. This author listed several plesiomorphies (viz., the presence of 3–4 simple veins stretching from CuA to the basitornal margin of the forewings and “ephemeropteroid” – dissimilar subimaginal claws) and the characteristics of unclear phylogenetic status for this genus (viz., rudimentary paracecereus), underlining also the necessity of additional study of the thoracic structures in the type specimen of B. oligocaenicus in order to clarify its systematic position.

The aim of this paper is the redescription and illustration of the holotype of B. oligocaenicus from W. Simon’s collection at the Museum für Naturkunde Berlin, which has been studied in 2004. Additionally, some remarks and illustrations on the first fossil representative of the genus Ameletus Eaton, 1885, earlier described by Kluge (2004), are given as well.

The drawings were made by means of a binocular microscope (Leica WILD M3Z) using a camera lucida (WILD 308700). Photographs were made with a Leica DC 200 camera mounted on a Leica MZ FL III microscope, and digitally processed in Adobe Photoshop 5.0 and Lucia G (Nikon) computer software.


**TAXONOMY**

**Ameletidae** McCafferty, 1991

**Baltameletus** Demoulin, 1968


*Baltameletus/g*: Kluge, 2004: 355 (within Anteritorna incertae sedis).

**Type species.** *Baltameletus oligocaenicus* Demoulin, 1968 by original designation.

**Diagnosis.** Male subimago. Of all known genera of the family Ameletidae, only *Baltameletus* is characterized by the presence of the following characteristics: (1) unpaired projection on vertex; (2) compound eyes strongly contiguous dorsally; (3) 2–3 mainly simple veins stretching from CuA to basitornal margin of the forewings.

**Baltameletus oligocaenicus** Demoulin, 1968 (Figs 1–6)


**Type material.** Holotype: male subimago in Eocene Baltic amber (MB.J 2248). Body well preserved, distinctly visible from from both lateral aspects. Holotype is originally labeled as: “Holotype Fam. Ephemeridae Demoulin 1968, Fig. 4 11” ; “G. Demoulin det., 1966 Baltameletus oligocaenicus sp. n. subimago”.

**Material examined.** Only the holotype.

**Description.** Measurements. See Table 1.

The color of body pale is yellow to yellowish brown. Head yellow, antennae brownish. Compound eyes divided into dorsal and ventral portions, and strongly contiguous dorsally (Fig. 2). Vertex with unpaired projection distinct and visible from anterior and both lateral (Figs 2–4, non-unique apomorphy according to Kluge 2004: 378).

Thorax darker than head. Most of right side of thorax damaged or lost. Mesonotal suture stretched backward medially. Anterior paracoxal suture complete (Fig. 4, see also Kluge 2004: 81, Fig. 21B, C). Latero-parapsidal suture of mesothorax relatively elongate, its distal part not visible (Figs 3–4). Pigmentation of thorax not preserved. Epimeron of mesothorax with a membranous area between anepimeron and katepimeron (Fig. 4, see also Kluge 2004: 81, Fig. 21C). Details of structure of sternum not generally discernable. Furcasternal protuberances contiguous, without median impression of furcasternum.

Wings opaque. Longitudinal veins dark. Cross veins poorly visible. Pterostigmatic area of forewings with simple cross veins only. MP triad of forewings well developed. MP₂ longer than iMP, connected with MP₁ and CuA by several cross veins (Fig. 1). Marginal intercalaries well developed between RSa₁ and MP₂, connected with longitudinal veins. Cubital field of forewings with 2 (in the left wing) and 3 (in the right wing) mainly simple veins stretching from CuA to basitornal margin of the wing (Fig. 1, see Kluge 2004: 82, Fig. 7C). Hind wings with costal projection, obtuse apically, as long as 0.33 of forewing length; RS, MA and MP triads well developed (Fig. 4).
Figures 1–4. *Baltameletus oligocaenicus* Demoulin, 1968, holotype (MBJ 2248), male subimago. (1) Right forewing in ventral view. Based on the original of Georges Demoulin (Deutsche Entomologische Zeitschrift, 1968, Band 15, Heft 1–3, Fig. 3b, Page 239). The changes (depicted in red) are discussed in the text in detail. (2) Head. (3) Right side of body. (4) Left side of body. The contour of Hydracarina larvae is not depicted.

Vp – protuberance of vertex, MPs – medioparapsidal suture, MNs – mesonotal suture, AEM / KEM – membranous area. Scale bars = 1 mm.
Legs well preserved. The leg segment measurements are given in Table 1. All tarsi 5-segmented, first segment fused with tibia. Tarsi of middle and hind legs shorter than tibiae, the first segment not the longest one (see Demoulin 1968: Fig. 3c, d). All claws dissimilar, with one pointed and the other one blunt.

Abdominal segments pale (the right side of abdomen partly damaged or lost). Lateral part of segment IX without any projection. Forceps with two distal segments. The structure of styliger plate not discernable. Paracercus lost, poorly preserved left cercus shorter than body.

Discussion. The holotype of *Baltameletus oligocaenicus* is a well-preserved specimen. However, only its left side is available for studying details of the body structure. On the right side of the specimen, the distal part of the thorax and lateral part of abdominal segments are not preserved. The ventral side of body is obscured due to an excrescence of amber. The distal portions of the
mesonotum and metanotum are not visible because of folded wings.

Demoulin (1968) gave only a brief description of the species *B. oligocaenicus* and did not provide details of the head structure. Demoulin’s illustrations (p. 239, figs. 3a, 3f) demonstrate the general appearance of the holotype from the left side and the enlarged depiction of the distal portion of its head with the attached larva of a parasite of the suborder Hydracarina (Arachnida: Acari). The presence of an unpaired protuberance on the vertex was not noted (in our illustrations the Hydracarina has been removed, see Figs 2–4). The structure of the compound eyes, which are clearly divided into dorsal and ventral portions and strongly contiguous dorsally in the holotype of *B. oligocaenicus* (Figs 2–4), was not described by Demoulin either.

In Demoulin’s paper (1968), the structure of the thorax of the holotype was described incompletely, and in his Fig. 3a (the general appearance), only the contour of thorax can be seen without any structural details.

Re-examination of the holotype confirms the presence of characteristics such as a posteriorly extended mesonotal suture, deep anterior paracoxal suture (preserved on the left body side only) and relatively elongate lateroparapsidal sutures. The details of the epimeron are clearly visible. We can also confirm the presence of a membranous area between the anepimeron and katepimeron. Ventrally, the thorax bears clearly contiguous furcasternal protuberances (Fig. 4).

Demoulin described and illustrated several unique characteristics in the venation of the forewings, which, in his opinion, easily distinguish *Baltameletus* from all other representatives of Siphlonuridae (Demoulin 1968: 238–239, 3b), viz. (1) the presence of iMP arising from CuA and connected by cross veins with MP1 and MP2, and (2) the availability of MP2 shorter than iMP, arising from CuA and disconnected with MP1. At the same time, Demoulin mentioned the limited visibility of the transverse venation.

In fact, the MP triad of *Baltameletus* forewings is typical of all Siphlonuroidea Banks, 1900, that is: iMP is distinctly shorter than MP2 and connected with MP1 by several cross veins. The bifurcation of MP1 and MP2 is relatively visible (Fig. 1, depicted in red). We also confirm the presence of 2–3 veins in the cubital field of the forewings, arising from CuA, and the presence of numerous marginal intercalaries between RSa1 and MP2 (Fig. 1, depicted in red). These structures were illustrated in part by Demoulin (1968). In contrast to Demoulin’s figure 3a, the MA and MP triads arise from a common stem.

The right hind wing was illustrated by Demoulin (1968) only schematically, without specification of transversal and RS venation. The details of this wing venation are not quite clear. However, all three triads of veins, viz. RS, MA and MP, are present and
Table. 2. The selected characters of adult males of extant and fossil genera of the family Ameletidae.

<table>
<thead>
<tr>
<th>Genera</th>
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Legend

I. Head characters
A. Eyes:
(0) strongly contiguous dorsally (Fig. 2, see also Zhou and Peters 2003: 347–348, Fig. 21);
(1) more or less separated (Godunko and Neumann 2006: 176, Figs 1, 2).
B. Vertex:
(0) with unpaired projection (Figs 2-4, see also Kluge et al. 1995: 118, Fig. 22, Kluge et al. 1995, 111, 113, Fig. 18, Kluge 2004: 81, Fig. 11A, C, Kluge 2004: 81, Fig. 11C); (1) without any projection (Godunko and Neumann 2006: 176, Figs 1, 2).

II. Thorax characters
C. Pigmented area of mesonotum (this character is not preserved in the type species of the genus Baltameletus):
(0) includes entire sublateroscutum and submedioscutum up to medioparapsidal suture (apomorphy of Ameletidae) (Kluge et al. 1995, 111, 113, Fig. 22, Kluge 2004: 81, Fig. 11B, Godunko and Neumann 2006: 179, Fig. 9);
(1) the arrangement of pigmented area is different.
D. Epimeron of mesothorax (this structure is not visible in the type species of the genus Electroletus):
(0) with membranous area between anepimeron and katepimeron (apomorphy of Ameletidae) (Fig. 4, Kluge et al. 1995, 111, 113, Fig. 18, Kluge 2004: 81, Fig. 11C);
(1) without membranous area.

III. Wing characters
E. Pterostigmatic area of forewings:
(0) with simple cross veins only (Fig. 1, Godunko and Neumann 2006: 176, Figs 1, 3);
(1) with forked cross veins (Demoulin 1951: 19, Fig. 11a, Ujhelyi 1960: 201, Fig. 5, Studemann et al. 1988: 315, Figs 51, 52); (2) with both above types of venation.
F. Cubital field of forewings:
(0) with 2–3 mainly simply veins stretching from CuA to basitornal margin of the wing (Fig. 1, Demoulin 1968: 239, Fig. 3b);
(1) with 4–8 occasionally forked veins stretching from CuA to basitornal margin of the wing (Kluge 2004: 82, Fig. 7C);
(2) with 1–2 intercalaries (Demoulin 1951: 19, Figs 1a, 1e, 11a, c, d, Ujhelyi 1960: 203, Fig. 4, Studemann et al. 1988: 315, Fig. 52a, Kluge 2004: 82, Godunko and Neumann 2006: 176, Figs 1–3).
G. Costal projection of hind wings:
(0) pointed apically (Demoulin 1951: 19, Fig. 11b, Ujhelyi 1960: 203, Fig. 4, Demoulin 1968: 239, Fig. 3b, Studemann et al. 1988: 315–316, Fig. 51b, Godunko and Neumann 2006: 176–177, Figs 2, 5);
(1) pointed or obtuse apically (Studemann et al. 1988: 315–316, Fig. 52b).

IV. Leg characters
H. Tarsi of middle and hind legs:
(0) longer than tibiae, the first tarsal segment being the longest one (Godunko and Neumann 2006: 176, Figs 1, 2);
(1) shorter than tibiae, the first tarsal segment not being the longest one (Table 1–2, Demoulin 1951: 15, Ujhelyi 1960: 202–203, Fig. 6, Demoulin 1968: 239, Figs 3a, d, Studemann et al. 1988: 315–316, Fig. 50f).

V. Genitalia characters*
I. Styliiger plate:
(0) with median protuberance (Godunko and Neumann 2006: 177, Figs 5, 6);
(1) with deep median incision (Ujhelyi 1960: 201, Fig. 1, Studemann et al. 1988: 311, Figs 48, 49, Kluge et al. 1995, 111, 113, Fig. 19, Kluge 2004: 51, 81, Fig. 11A).

* The genitalia structure of type species of both fossil genera is only partly visible. Besides, as these taxa have been described on the basis of the male subimago, it is impossible to ascertain the presence of the membranous area of styliiger plate, which is available in the male imago only (apomorphy of Ameletidae) (see Kluge et al. 1995: 111, 113, Fig. 19, Kluge 2004: 81, Fig. 11B, C).
The relationships of recent genera *Ameletus* and *Metreletus* Demoulin, 1951 of the family Ameletidae have been studied by several authors. Demoulin (1951, 1952) analyzed some morphological details, including the structure of the surface of the egg chorion, in *Metreletus* (this genus was designated by the author for three species, earlier attributed to *Metretopus* Eaton, 1901), comparing it with *Ameletus*, and also with other genera belonging to the family Metrettodidae (e.g. *Metretopus* and *Siphloplecton* Clemens, 1915). Studemann et al. (1988) proposed the distinguishing combination of morphological characteristics of male and female imago, and generalized information on the structure of the egg chorion in two species using electron microscopy. Kluge et al. (1995) stated the basic distinguishing characteristics of Ameletidae and made brief comments on the taxonomic composition of this family, however without a detailed description of the relationship between both extant genera. Finally, Kluge (2004) listed apomorphies and plesiomorphies of larvae and imagoes of *Ameletus* and *Metreletus*, and data on their general distribution and species composition. In the same work, the author for the first time presented brief information on availability of the genus *Ameletus* in fossil condition (see below).

Godunko and Neumann (2006) described the monotypic genus *Electroletus* Godunko and Neumann, 2006 (type species *E. soldani* Godunko and Neumann, 2006) from the Eocene Baltic amber, and placed this genus within the family Ameletidae on the basis of the presence of traces of a pigmented area on sublateroscutum and submedioscutum of the mesonotum (a reliable autapomorphy of Ameletidae) in the holotype (male subimago). The diagnosis of the genus *Electroletus* is based on the peculiarities of the morphological structure of pterostigmatic area and cubital field of forewings, tarsal segments and styliger plate. The authors also analyzed in detail the relationship between this fossil genus and extant genera of Ameletidae (Godunko and Neumann 2006: 178–179).

Summarized data on the relationships between all genera of the family Ameletidae are given in Table 2.

The present composition of the family Ameletidae includes four genera. The family includes two exclusively fossil monotypic genera, *Baltameletus* and *Electroletus*, from the Eocene Baltic amber (40–50 my bp). The genus *Ameletus* (generic synonyms: *Chimuра* Navás, 1915; *Palaeoameletus* Lestage, 1940) includes more than 50 extant species distributed in the Holarctic and Oriental Regions, and one unnamed fossil species, from Eocene Baltic amber (see below). The extant genus *Metreletus* includes a single European species (*M. balcanicus*).
Material examined. Female imago in the Eocene Baltic amber, Museum of Natural History of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences (Kraków, Poland), inventory number MP 1/03/UK/2, coll. Wiesław Krzemiński. The specimen is clearly visible in lateral view, its thorax being slightly crumpled and abdomen damaged distally. The same piece of amber contains about 40 specimens of Diptera: Nematocera. Measurements are in Table 3.

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure7-8.jpg}
\caption{Figures 7–8. \textit{Ameletus} sp., inventory number MP 1/03/UK/2, Museum of Natural History of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, female imago. (7) Right side of body. (8) Forewings. Without scale.}
\end{figure}
The male imago from the collection mentioned, belonging to the genus *Ameletus*, was examined by us in 2003. The first brief information on this specimen was published by Kluge (2004: 81).

Evidently, the specimen can be attributed to the genus *Ameletus* on the basis of the following characters: (1) epimeron of mesothorax with a membranous uncolored area between sclerotized and pigmented anepimeron and katepimeron; (2) first tarsal segment fused with tibia, subequal to second segment; (3) forewing length 7 mm (in other species of *Ameletus* forewing length ranges from 7 to 17 mm); (4) cubital field of forewings with 4 or 5 veins arising from CuA (in other species of *Ameletus* cubital field with 4–8 such veins); (5) all tarsal claws dissimilar. The distal part of the abdomen is damaged. The cerci and paracercus are lost.

In the majority of known species of *Ameletus* adult females lack diagnostic characters. Thus, this fossil specimen cannot be determined to species level.

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**References**


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