

Revision of fossil Metretopodidae (Insecta: Ephemeroptera) in Baltic amber – Part 1: Type specimens of hitherto described fossil species of *Siphloplecton* CLEMENS, 1915 and *Metretopus* EATON, 1901; with description of four new fossil species of *Siphloplecton*

ARNOLD H. STANICZEK & ROMAN J. GODUNKO

Abstract

In a first step to revise the fossil species of the mayfly family Metretopodidae, a historical overview and redescription of the type specimens of all hitherto described fossil species is given. All preserved specimens of *Siphloplecton macrops* (PICTET-BARABAN & HAGEN, 1856), *S. jaegeri* DEMOULIN, 1968, *Siphloplecton* spp., *Metretopus? henningseni* DEMOULIN, 1965, and *M. trinervis* DEMOULIN, 1968 are redescribed along with the description of *Siphloplecton picteti* sp. nov., *S. barabani* sp. nov., *S. hageni* sp. nov., *S. demoulini* sp. nov., and further specimens of the genus *Siphloplecton*.

Keywords: Fossil insects, mayflies, Ephemeroptera, Siphonuroidea, Metretopodidae, *Metretopus*, *Siphloplecton*, new species, Baltic amber, Eocene.

Zusammenfassung

In einem ersten Schritt zur Revision der fossilen Arten der Eintagsfliegenfamilie Metretopodidae erfolgt ein historischer Abriss und die Neubeschreibung der Typusexemplare aller bisher beschriebenen fossilen Arten. Alle erhalten gebliebenen Exemplare von *Siphloplecton macrops* (PICTET-BARABAN & HAGEN, 1856), *S. jaegeri* DEMOULIN, 1968, *Siphloplecton* spp., *Metretopus? henningseni* DEMOULIN, 1965, und *M. trinervis* DEMOULIN, 1968 werden erneut beschrieben, einhergehend mit der Neubeschreibung von *Siphloplecton picteti* sp. nov., *S. barabani* sp. nov., *S. hageni* sp. nov., *S. demoulini* sp. nov. und weiterer Exemplare der Gattung *Siphloplecton*.

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1. Introduction

Metretopodidae TRAVER, 1935 is a small, monophyletic mayfly family with Holarctic distribution and presumably boreal origin (BERNER 1978, KLUGE 2004). It comprises 11 extant species in the genera *Metretopus* EATON, 1901 (one Holarctic and two Palearctic species), *Siphloplecton* CLEMENS, 1915 (seven Nearctic species), and *Metreplecton* KLUGE, 1996 (one Palearctic species).

There are only few contributions on fossil Metretopodidae in Baltic amber: DEMOULIN (1965) described *Metretopus? henningseni* from an isolated right forewing. *Metretopus trinervis*, a second species, was described by DEMOULIN (1968) from male and female subimaginal specimens. In this contribution, he also reinvestigated the preserved type specimens of *Palingenia macrops* described by PICTET-BARABAN & HAGEN (1856). DEMOULIN (1968) transferred this species to *Siphloplecton* and assigned “hololectotype” and two “paralectotypes” from the original type series. He also assigned an allotype from new material and attributed further specimens to *S. macrops*. DEMOULIN (1968) finally also described *S. jaegeri* and referred to another female specimen as *Siphloplecton* sp. Two years later, DEMOULIN (1970) reported new specimens of fossil Metretopodidae that he attributed to *Siphloplecton ?macrops* and *S. jaegeri*. Some of DEMOULIN’s (1965, 1968, 1970) nomenclatorial decisions turned out to be problematical, especially his associations of male and female specimens to the same species without being able to affirm this by discriminating characters.

Today there are many more morphological characters known to distinguish the different species. When we got hold of new fossil material of Metretopodidae, we soon realised that we would first need to clarify the status of hitherto described fossil species. In order to stabilise nomenclature before working on new material, we give here an overview of the taxonomical history of fossil Metretopodidae. All preserved material is redescribed and critically evaluated. In this context we also describe four new species out of the old material, namely *Siphloplecton picteti* sp. nov., *S. barabani* sp. nov., *S. hageni* sp. nov., and *S. demoulini* sp. nov., and another four specimens of the genus *Siphloplecton*.

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2. Material and methods

Drawings were made with a camera lucida on a Olympus SZX7 or a Leica S8 APO stereo microscope. Photographs of fossils were taken through a Leica Z16 APO Macroscope, processed with Leica Application Suite™ Version 3.1.0 to obtain combined photographs with extended depth of field, and subsequently enhanced with Adobe Photoshop™ CS3. The fragile and brittle holotype of *M.? henningseni* was embedded into resin to prevent further damage.

Acronyms of depositories

GZG	Geowissenschaftliches Zentrum der Universität Göttingen, Germany
MNB	Museum für Naturkunde, Berlin, Germany
MNHN	Muséum national d’Histoire naturelle, Paris, France
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany
ZMUC	Zoologisk Museum, Københavns Universitet, Copenhagen, Denmark

3. Systematic palaeontology

Order Ephemeroptera HYATT & ARMS, 1890

3.1. Family Metretopodidae TRAVER, 1935

Metretopodidae TRAVER, 1935 comprise 11 extant species in three genera (BERNER 1978, KLUGE 1996, TIUNOVA 1999):

- (1) *Metretopus* EATON, 1901 including the Holarctic species *Metretopus borealis* (EATON, 1871) and the Palearctic species *M. alter* BENGTTSSON, 1930 and *M. tertius* TIUNOVA, 1999.
- (2) *Siphloplecton* CLEMENS, 1915 including seven Nearctic species in two species groups:
 - (a) *basale* species group including *S. basale* (WALKER, 1853); *S. simile* BERNER, 1978; *S. brunneum* BERNER, 1978; *S. speciosum* TRAVER, 1932;
 - (b) *interlineatum* species group including *S. interlineatum* (WALSH, 1863); *S. costalense* SPIETH, 1938; *S. fuscum* BERNER, 1978.
- (3) *Metreplecton* KLUGE, 1996 including the single Palearctic species *M. macronyx* KLUGE, 1996.

The monophyly of the family is established by numerous larval autapomorphies. Larvae of Metretopodidae are readily identified by their unique, bifurcate foreclaws (cf. KLUGE 2004, fig. 22C). Other presumably autapomorphic characters are related to the posteriorly bent apical parts of glossae and paraglossae, reduction of lacinial incisivus (cf. STANICZEK 2001, fig. 92: IncL), posteromedial shift of lateral galeal row of setae (cf. STANICZEK 2001, fig. 95: Sga; apical-ventral row sensu KLUGE 2004: fig. 22D), and reduced costal ribs of gills I–III.

Winged stages can only be distinguished from all other Ephemeroptera by the combination of following characters: mesonotal suture nearly transverse or medially bulged, lateroparapsidal suture elongate, contiguous prosternal protuberances, tibioapatellar suture present only in middle and hind legs, first tarsomere longest of all tarsomeres, fused to tibia at least in middle and hind leg, praetarsus with one blunt and one hooked claw, cubital field of forewing with one to four intercalaries, hind wing with three triads, costal process present, and paracercus vestigial (KLUGE 2004).

3.1.1. Genus *Siphloplecton* CLEMENS, 1915

Siphloplecton is characterized in the winged stages by the presence of two pairs of intercalaries in the cubital field of forewing (Figs. 1a, 2a). Occasionally there may be only three cubital intercalaries present. MP_2 is basally strongly divergent from MP_1 .

Extant species of the *S. basale* species group (Fig. 1a–c) in the male imago generally with strongly pigmented wing area (Fig. 1a), outer margin of foretibiae with broad, apically brush-like spines, penis (Fig. 1b) generally appears more jolted (*basale* type sensu BERNER 1978): each penis lobe with globular to quadrate outline, penis medially only moderately incised. Penis at half length laterally constricted to form an angle of about 90°.

Extant species of the *S. interlineatum* species group (Fig. 2a–c) in the male imago generally with weakly pigmented wing area (Fig. 2a), outer margin of foretibiae with thick, pointed spines, penis (Fig. 2b) generally appears more elongated (*interlineatum* type sensu BERNER 1978): each penis lobe with triangular outline apically, penis medially deeply incised. Penis at half length laterally constricted to form an angle of more than 90°.

3.1.1.1. *Siphloplecton macrops* (PICTET-BARABAN & HAGEN, 1856) (figs. 38a–e in DEMOULIN 1968)

- 1846 *Palingenia*. – PICTET, p. 108 (first information without use of species name).
 1854 *Palingenia macrops* PICTET et BERENDT. – PICTET, p. 371 (nomen nudum, because without description).
 1854 *Palingenia macrops* PICTET. – HAGEN, p. 227 (nomen nudum, because without description).
 1856 *Palingenia macrops*. – PICTET-BARABAN & HAGEN, p. 74, Tab. VI, fig. 2. (b.), Tab. VIII, fig. 5 (first description).
 1856 *Palingenia macrops*. – ANONYMOUS, p. 621 (book review of BERENDT 1856 with species list).
 1856 *Palingenia macrops*. – GIEBEL, p. 182 (species list).
 1857 *Palingenia macrops*. – MARSCHALL, p. 113 (perennial species index to journal Sitzungsberichte und Abhandlungen des Wiener zoologisch-botanischen Vereines).
 1861 *Palingenia macrops*. – BOITARD, p. 430 (species list).

- 1861 *Palingenia macrops*. – LEONHARD & BRONN, p. 395 (perennial species index to journal Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde).
 1871 *Polymitarcys macrops*, HAG.; in *Palingenia*, HAG. – EATON, p. 36 (species list), p. 45 (distribution), p. 61 (description).
 1888 *Palingenia* [*macrops*, PICT. (1854)]. – EATON, p. 351 (species list).
 1891 *Palingenia macrops*. – SCUDDER, p. 356 (species list).
 1907 *Palingenia macrops* PICTET. – HANDLIRSCH, p. 906 (species list), p. 1409 (index).
 1928 *Palingenia macrops*. – BACHOFEN-ECHT, fig. 21 (photograph).
 1955 *Palingenia macrops* PICTET. – DEMOULIN, p. 1 (species list).
 1968 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – DEMOULIN, p. 249 (nov. comb.), p. 274 (designation of holotype), fig. 38a–e (holotype).
 1974 *Siphloplecton macrops* [in partim]. – DEMOULIN, p. 4 (correction of EATON's placement of *Palingenia macrops* within *Polymitarcys*, and subsequent citations by THERNOVA (1962) and EDMUNDS (1972) as fossil *Ephoron*).
 1978 *Siphloplecton macrops* (PICTET) [in partim]. – LARSSON, p. 81 (review of generic attribution).
 1987 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – HUBBARD, p. 46 (list of synonymy).
 1998 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – WEITSCHAT & WICHARD, p. 94 (species list).
 2004 [*Palingenia*] *macrops* PICTET & HAGEN 1856 [in partim]. – KLUGE, p. 359 (in Euplectoptera inc. sed.), p. 420 (index).
 2006 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – GODUNKO & NEUMANN, p. 178 (discussion of species composition).
 2009 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – WICHARD et al., p. 291 (species list).

3.1.1.1.1. Historical overview on the description of *S. macrops*

The first information on a fossil specimen of Metretopodidae can be traced back to a note by PICTET (1846) referring to fossil mayflies in amber from BERENDT's collection (then Danzig). In this note, PICTET mentioned that "... nous y avons ... trois Éphémérines, appartenant aux genres *Baëtis*, *Palingenia* et *Potamanthus*". In a later contribution, PICTET (1854) again referred to these three fossil species, but for the first time he attributed a binominal name to each of them. Important in our context is the mentioning of a fossil species of *Palingenia*: "Les fragments d'ambre que M. BERENDT m'avait envoyés en contenaient trois especes. J'en ai rapporté une au genre *Palingenia*, BURMEISTER, sous le nom de *P. macrops*, PICTET et BERENDT ...". However, there was neither a description nor a drawing provided in this contribution. PICTET later intended to publish a detailed description on 120 insect specimens of BERENDT's collection, but was then occupied with other duties. So PICTET passed his manuscript on to HAGEN, who in the meantime had started to work on BERENDT's collection. As the col-

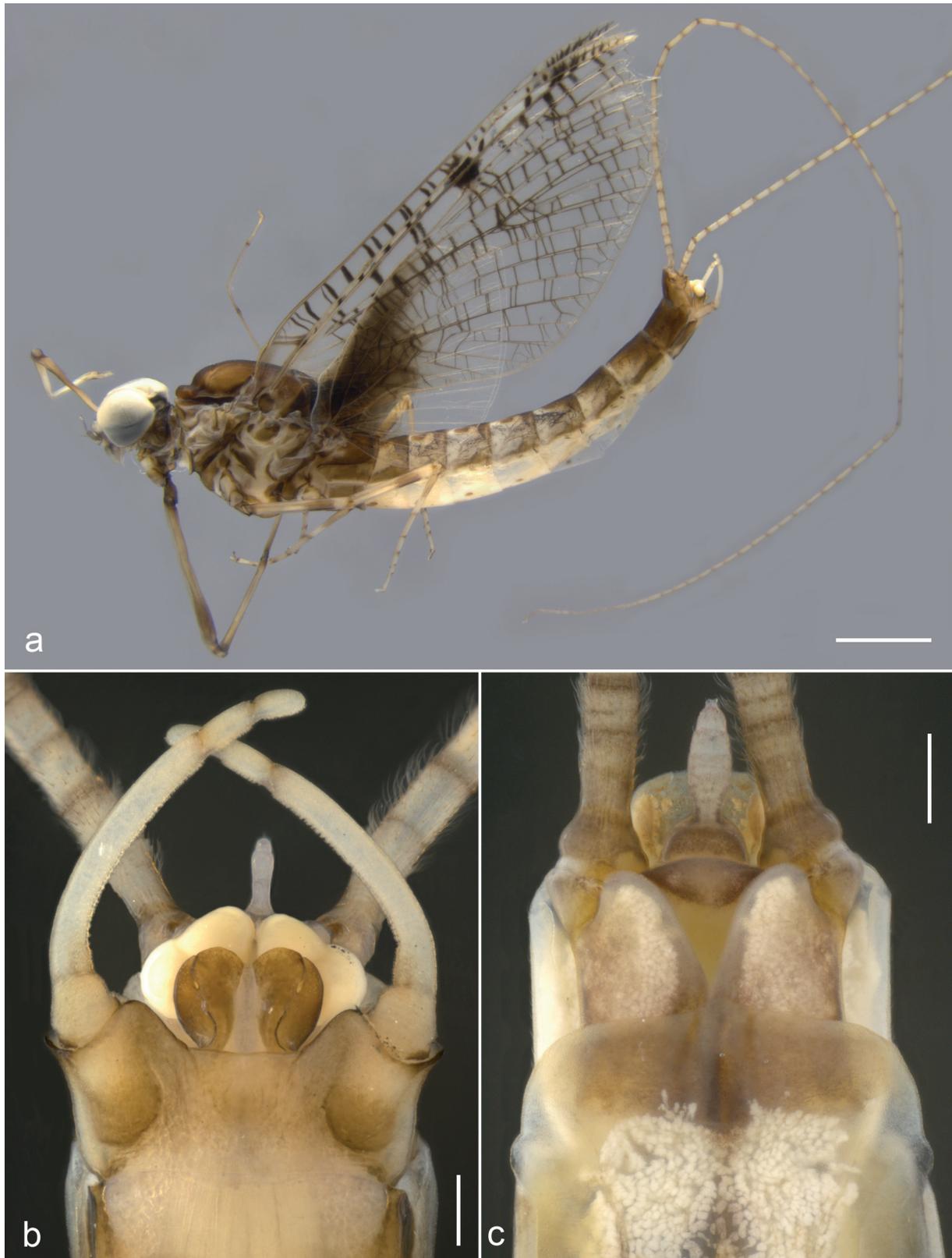


Fig. 1. *Siphloplecton basale* (WALKER, 1853). – **a.** Male imago in lateral view. **b.** Male genitalia in ventral view. **c.** Female genitalia in ventral view. – Scale lines 2 mm (a), 0.2 mm (b, c).

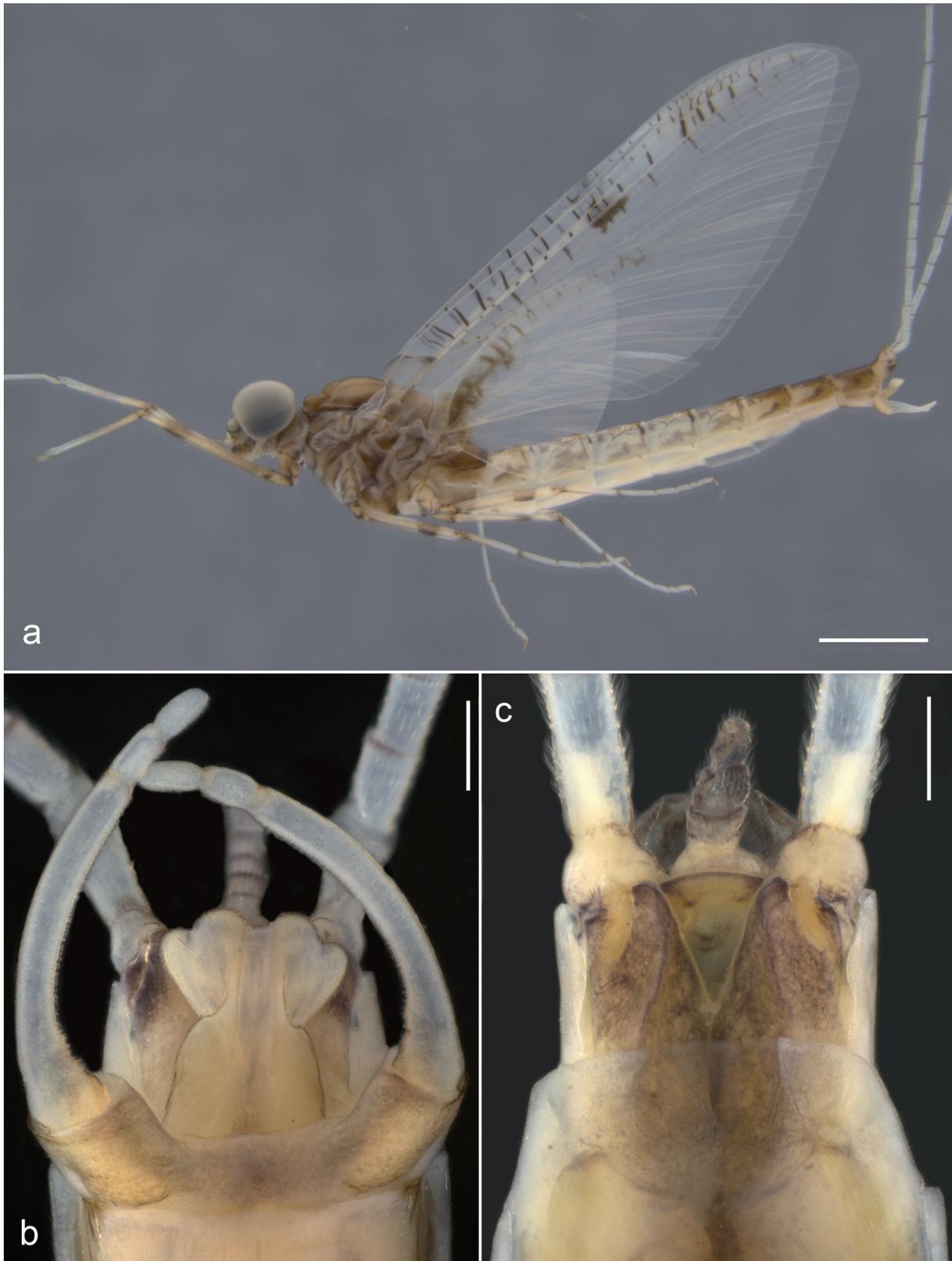


Fig. 2. *Siphloplecton interlineatum* (WALSH, 1863). – **a.** Male imago in lateral view. **b.** Male genitalia in ventral view. **c.** Female genitalia in ventral view. – Scale lines 2 mm (a), 0.2 mm (b, c).

lection was still provided with PICTET's original labeling, HAGEN (1854) referred to the names given by PICTET, attributing 46 specimens of fossil mayflies to five different species in three above mentioned genera, among them also *Palingenia macrops*. However, also HAGEN (1854) neither provided a description nor a drawing. Only two years later, PICTET-BARABAN & HAGEN (1856) published the first formal description of *Palingenia macrops* in a chapter of BERENDT's monumental book on fossil insects. This contribution is crucial (and problematic) in several respects because it affects the authorship of *P. macrops* as well as the discussion about the type fixation that will be discussed below (see 3.1.1.1.2.). In the chapter on Neuroptera (including mayflies at that time) PICTET-BARABAN & HAGEN (1856) are listed as authors, but in fact the paragraph on mayflies was solely finalised by HAGEN based on PICTET's earlier manuscript. However, dealing with *Palingenia macrops*, HAGEN explicitly mentioned "Die Schilderung ist eine wörtliche Übersetzung des Textes von PICTET." This was the reason for some recent workers to attribute the authorship of *P. macrops* to PICTET alone, based on chapter 11, Article 50.1 and Recommendation 51 E of ICZN, thus citing the name as *Palingenia macrops* PICTET, 1856 (see DEMOULIN 1968) or as *Palingenia macrops* PICTET in PICTET-BARABAN & HAGEN, 1856 (see HUBBARD 1987). Despite of HAGEN's remark in the beginning of the paragraph, the description that follows is actually supplemented with HAGEN's own and different observations on the male imago, thus correcting PICTET's earlier notes. For instance, HAGEN pointed to mistakes in PICTET's drawing of the genitalia (tab. VI, fig. 2b) and wings (tab. VI, fig. 2), and HAGEN even included his own figure of the left forewing with the description (tab. VIII, fig. 5). HAGEN's amendments along with the addition of his own figure are essential parts of the description of *P. macrops*, so in our view according to Article 50 of ICZN (ICZN 2001), the authorship must be attributed to both PICTET and HAGEN.

Another problem concerns the different usage of PICTET's name in this contribution. François Jules PICTET emanated from a large family of intellectuals from Geneva (see CANDAUX 1974 for the family history of PICTET). To distinguish the different family members it was common use in Geneva to add the wife's maiden name to one's own name (PETERS et al. 1980). So F. J. PICTET's father was known as Jean Pierre PICTET-BARABAN, and once F. J. PICTET was married he called himself FRANÇOIS-JULES PICTET DE LA RIVE. However, after marriage he continued to publish under "F. J. PICTET", but for some reason unknown to us, in the contribution to BERENDT (1856) his father's surname is used to read him as F. J. PICTET-BARABAN. Whether this was an unintentional mix-up with his father's surname, possibly done by the editor or publisher, or an intentional name change by F. J. PICTET himself remains unclear. The ICZN gives no clear instruction on how to deal with this problem,

so we decided to use the published name PICTET-BARABAN as authorship, leaving the correct name as *Palingenia macrops* PICTET-BARABAN & HAGEN, 1856.

3.1.1.1.2. The problem of type designation in *S. macrops*

While we now have clarified the authorship of *P. macrops*, there remain some difficulties regarding the type fixation. PICTET-BARABAN & HAGEN (1856), as usual at that time, did not designate a holotype. Their contribution to *P. macrops* is divided into two parts:

While it is stated right away in the first part that there was a series of altogether 11 specimens available (without specification of sex and life stage), the actual description obviously focuses on a single adult male: "... denn das Exemplar, welches mir vorliegt (es ist ein Männchen), zeigt deutlich ..." and "... in dem einzigen Männchen, welches PICTET untersuchen konnte ...". The two figures drawn by PICTET (tab. VI, fig. 2, 2(b.)) and the added wing drawing by HAGEN (tab. VIII, fig. 5) explicitly refer to this specimen. However, there must have been more male imagines available to HAGEN because DEMOULIN (1968), who reinvestigated the remains of the type series (see below), reported three male imagines from this series labeled by HAGEN.

In the second part HAGEN added the description of a male subimago without illustration that he also assigned to *P. macrops*.

Only some 112 years after the original description, DEMOULIN (1968) in his second contribution to mayflies in Baltic amber realised the affinities of *P. macrops* to Metztopodidae and transferred *P. macrops* to the genus *Siphloplecton*.

At that time the BERENDT collection had been transferred to the MNB but out of the original type series of 11 specimens only 3 specimens had survived:

Albeit then in a very bad condition and fragmented, DEMOULIN could identify the male imago that had been figured in the first part of PICTET-BARABAN & HAGEN (1856). This specimen was forwarded to him by J. ILLIES (Schlitz) who had discovered it (along with a specimen of *Paraleptophlebia prisca*) among fossil Plecoptera in the amber collection of MNB. DEMOULIN (1968) redescribed and refigured the specimen (fig. 38) and designated it as "hololectotype" (= lectotype) in an addendum he attached to his original publication.

The second specimen had been labeled by HAGEN as subimago, but DEMOULIN (1968) described it as another male imago (fig. 14a) and designated this specimen as paralectotype. DEMOULIN concluded that this was probably the specimen that had been described as male subimago by HAGEN in the second part of PICTET-BARABAN & HAGEN (1856), but we do not consider this to be likely. HAGEN had clearly stated that his subimaginal specimen was equipped

with grey, dull wings having tiny hairs on the surface and hind margin, and also hairs on the cerci. It is more probable that this specimen was one of the remaining specimens of the type series, but as HAGEN did not picture his subimago, there is no proof of this assumption.

The third specimen from the BERENDT collection with HAGEN's original labeling was another male imago. DEMOULIN (1968) also redescribed and figured this specimen (fig. 14b, c) and also designated it as paralectotype.

As the remaining 8 specimens of *S. macrops* from the BERENDT collection were already lost in 1968, DEMOULIN also included two female imagines of *Siphloplecton* (figs. 15, 16) from the W. SIMON collection (MNB) and another two female imagines (figs. 17a, b) from the STANTIEN & BECKER collection (then SMNS) in his contribution (DEMOULIN 1968) and assigned them to *S. macrops*. Moreover, DEMOULIN (1968) designated one of the female imagines of the W. SIMON collection (fig. 15) as allotype of *S. macrops*. Finally, DEMOULIN (1970) described an additional specimen from the BURSEY collection (MNHN) as *Siphloplecton ?macrops* and also described a new fossil species *S. jaegeri* out of material from this collection.

When we started to work on new fossil material of Metretopodidae, it soon became clear that a lot of the new material we were dealing with could be attributed neither to *Siphloplecton macrops* nor to *S. jaegeri*. Having dealt with the complicated history of fossil *Siphloplecton* in literature we soon realised that we had to take a close look at the original material to clarify the identity of the species before describing new ones. Unfortunately, most of the original material has to be considered lost. Of the three specimens of the *S. macrops* type series (PICTET-BARABAN & HAGEN 1856) that were still available to DEMOULIN (1968), there is only one male imago (designated as paralectotype by DEMOULIN 1968, fig. 14b, c) present in the MNB today. The second paratype and the “hololectotype” designated by DEMOULIN (1968) – the latter already fragmented in 1968 – have to be considered lost. The inventory book of the MNB contains a remark that all BERENDT specimens had been returned to the amber collection from DEMOULIN. However, the “hololectotype” of *S. macrops* (as well the specimen of *Paraleptophlebia prisca*) unfortunately could not be traced again, despite of thorough search in the MNB amber collection. It was definitely also not among the remaining amber loans of ILLIES after his death (pers. comm. P. ZWICK, Schlitz). At least the two female specimens (one of which was designated as allotype by DEMOULIN 1968, fig. 15) of the SIMON collection could be located in the MNB. The pieces of the STANTIEN & BECKER collection housed at the SMNS in DEMOULIN's times went back to the GZG. There we could only locate one of the two female imagines described by DEMOULIN (1968).

Given the fact that there is a much greater variety of fossil *Siphloplecton* species than thought by DEMOULIN

(1968), his designations are highly problematical. Neither do we know if all the 11 specimens of the original type series from the BERENDT collection indeed were conspecific nor do we know if the female specimen designated as allotype by DEMOULIN (1968) is conspecific with the “hololectotype” designated by DEMOULIN (1968) that with near certainty is lost. Moreover, DEMOULIN's (1968) designation of an allotype taken not from the original type series in our view was definitely not covered by any rule of the ICZN. The poor original description of PICTET-BARABAN & HAGEN (1856) and the poor condition of the lost “hololectotype” do not allow any conclusion on the conspecificity of the only remaining specimen of the type series with the “hololectotype”.

Taken all these facts into account, we conclude that:

- (1) The name of *S. macrops* (PICTET-BARABAN & HAGEN, 1856) has to be restricted to the lost “hololectotype”.
- (2) The only surviving male imago of the type series of *S. macrops* has to be reinvestigated and to be attributed to a new species (see 3.1.1.2.).
- (3) The two surviving female specimens of the W. SIMON collection (MNB) have to be reinvestigated and attributed to a new species (see 3.1.1.3. and 3.1.1.4.).
- (4) The single surviving female specimen of the BURSEY collection (MNHN) has to be reinvestigated and to be attributed to a new species (see 3.1.1.5.).
- (5) The two surviving female specimens of the STANTIEN & BECKER collection (GZG) have to be reinvestigated (see 3.1.1.7.).

3.1.1.2. *Siphloplecton picteti* sp. nov.

(fig. 14b, c in DEMOULIN 1968)

Fig. 3a, 3b

1968 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – DEMOULIN, p. 250, fig. 14b, c (redescription, designation of paralectotype).

For remaining synonymies see 3.1.1.1.

Holotype: Male imago designated by DEMOULIN (1968: 250, fig. 14b, c) as paralectotype of *S. macrops*, originally labeled: “Paralectotype”; “G. DEMOULIN ver.: 1966 *Siphloplecton macrops* (Pictet) ♂ imago DEMOULIN, 1968, fig. 14b.”; “*Palinogenia macrops* mas.”. BERENDT collection, MNB, MB.I.2250 (Fig. 3a, b).

Stratum typicum: Eocene, Baltic amber.

Etymology: Named in honour of Swiss entomologist FRANÇOIS-JULES PICTET DE LA RIVE, one of the first mayfly experts.

Description. – Very damaged male imaginal specimen without head, thorax and legs (Fig. 3a, see also DEMOULIN 1968, fig. 14b). Only fragments of wings, part of abdomen (at least segments II–X, with partly damaged segment VIII), one cercus and genitalia (Fig. 3b) are preserved (see also DEMOULIN 1968, fig. 14c), so measurements could not be taken.

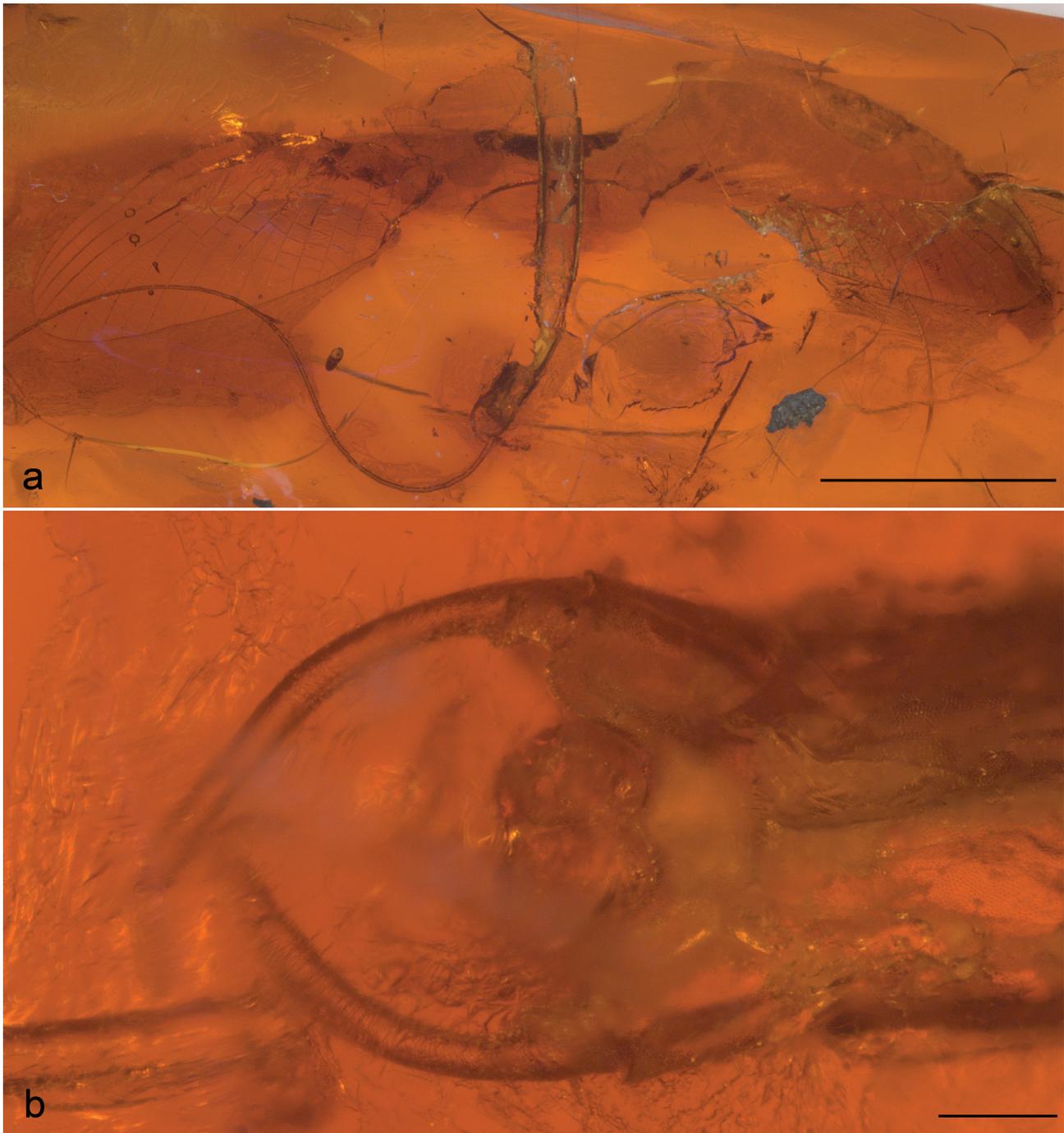


Fig. 3. *Siphloplecton picteti* sp. nov., holotype, male imago. – **a.** General ventral view. **b.** Genitalia in ventral view. – Scale lines 5 mm (a), 0.2 mm (b).

General colours of preserved parts of body pale, yellowish-brown.

Preserved apical part of right and left forewing with anastomosed veins of pterostigma (Fig. 3a and DEMOULIN 1968, fig. 14b). Apical part of right forewing with well pre-

served area between Sc and CuA. Proximal part of anterior cubital intercalary vein and also trace of posterior cubital intercalary vein preserved, forming a pair of intercalaries within the cubital field typical for *Siphloplecton*. Fragment of right hind wing with distal part of all three triads of

veins preserved. All preserved parts of wings translucent; no pigmentation around transversal veins visible.

Stylicher plate angulate, medioapically deeply and broadly incised; incision with small, triangular, central projection. Medially of each gonostylus, lateral parts of stylicher plate rounded and slightly protruding. Forceps 4-segmented, segment 2 longest, segment 4 approximately 3.80× as long as wide. Basal segment of forceps basally narrower than adjoining part of stylicher plate, medioapically with projection. Penis lobes distinctly rounded at tips, slightly expanding laterally, medially contiguous at entire length. Medial and lateral penis sclerites rounded.

DEMOULIN (1968: 250) describes the stylicher plate as “... en accolade (lobes latéraux proéminents, partie moyenne creusée en demi-cercle avec proéminence médiane)...”.

Discussion. – The presence of at least one pair of intercalaries in the cubital field of forewing, together with shape of stylicher plate and penis lobes, places this fossil specimen within the genus *Siphloplecton*.

S. picteti sp. nov. can be separated from the fossil species *S. jaegeri* by (1) shape of stylicher plate with small central and lateral projections (in contrast to the deeply incised stylicher plate and markedly broader lateral projections of *S. jaegeri*), and by (2) quadrangular shape of penis lobes rounded at tip and medially contiguous at entire length (in contrast to the elongated and medially incised penis of *S. jaegeri* with its apically triangular shape of penis lobes; penis lobes of the latter species only with inconspicuous incision between lateral and medial penis sclerite) (see DEMOULIN 1968: 253, fig. 18a).

S. picteti sp. nov. can be preliminary placed within the *S. basale* species group on the base of its penis structure (see Fig. 1b and BERNER 1978: 105, figs. 7–9, BERNER & PESCADOR 1988: 65, figs. 50, 51). At the same time, this new species can be distinguished from all Recent representatives of *Siphloplecton* by the shape of the stylicher plate with presence of a distinct, median, triangular pointed projection, a distinctly narrower basal forceps segment bordering with the apical part of stylicher plate, and lateral triangular projections of the stylicher plate (Figs. 1b, 3b). Presence or absence of spines on the outer margin of foretibia could not be determined since no legs are preserved in this specimen.

Both *S. picteti* sp. nov. and *S. jaegeri* (see 3.1.1.5.) have some similarities in the shape of the stylicher plate together with the Recent species *Metreplecton macronyx* (KLUGE 1996: 79, fig. 22). The two fossil species can be distinguished from the latter by the shape of penis lobes and the presence of more than one cubital intercalary vein in the forewing.

3.1.1.3. *Siphloplecton barabani* sp. nov.

(fig. 15a–d in DEMOULIN 1968; fig. 4a, b in DEMOULIN 1970)

Figs. 4–7; Tabs. 1, 2

1968 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – DEMOULIN, p. 249 (description, designation of allotype), fig. 15a–d.

1970 *Siphloplecton jaegeri* DEMOULIN, 1968 [in partim]. – DEMOULIN, p. 4, fig. 4a, b.

For remaining synonymies see 3.1.1.1.

Holotype: Female imago designated by DEMOULIN (1968: 250, fig. 15a–d) as allotype of *S. macrops*, originally labeled: “Allotype Fam. Ephemerae DEMOULIN, 1968, 15 (S 251) 8”; “G. DEMOULIN det., 1966 *Siphloplecton macrops* (Pictet) ♀ imago”. SIMON collection, MNB, MB.I.2236 (Figs. 4, 5).

Paratype: Female imago, DEMOULIN (1970: 4, fig. 4a, b), originally labeled: “G. DEMOULIN det., 1968 *Siphloplecton macrops* (PICTET) ♀ imago”; “G. DEMOULIN det., 1969 *Siphloplecton jaegeri* DMLN. ♀”; “4486”; “Ephémère”. BURSEY collection, MNHN, Nr 4486 (Figs. 6, 7).

Stratum typicum: Eocene, Baltic amber.

Etymology: Named in honour of Swiss entomologist FRANÇOIS-JULES PICTET DE LA RIVE, one of the first mayfly experts. His mother’s maiden name, BARABAN, was cited as second part of PICTET’S name in PICTET-BARABAN & HAGEN (1856).

Description of holotype. – Well preserved female imago (except of hind legs). For measurements see Tab. 1.

General colour of body pale, yellow to light-brown (Fig. 5a).

Eyes (compared to male imagines of *Siphloplecton*) relatively small, medially well separated. Ocelli with traces of dark pigmentation. Thorax with elongated lateroparapsidal suture (but hardly visible). Mesonotal suture medially slightly bulged (Fig. 4a). Furcasternal protuberances of mesothorax contiguous (Fig. 4b). Wings well preserved. Proportions of right forewing not distorted, entire wing well visible from dorsal and ventral sides (Fig. 4c). Left forewing twisted, and only its distal part can be observed (Fig. 5b). Forewings hyaline, translucent. Pterostigma with several anastomosed cross veins. No pigmentation around transversal veins visible. Base of MP₂ only slightly bent towards CuA. Cubital field with 2 pairs of intercalaries. Numerous cross veins (partly anastomosed) between iCu and CuA. Anal field with simple veins. Hind wings well-developed, 0.56× of forewing length, costal process bluntly pointed and small (Fig. 5c).

Measurements of leg segments in Tab. 1. First tarsal segment of forelegs is the longest one, not fused with tibia. First tarsal segments of middle legs longest, but fused with tibia. Tibia of middle legs with trace of tibiopatellar suture. Tarsi in all preserved legs 5-segmented. All tarsal claws are dissimilar with one hooked and one blunt claw.

Abdomen well preserved, same colour as body. Subanal and subgenital plates figured by DEMOULIN (1968: 251,

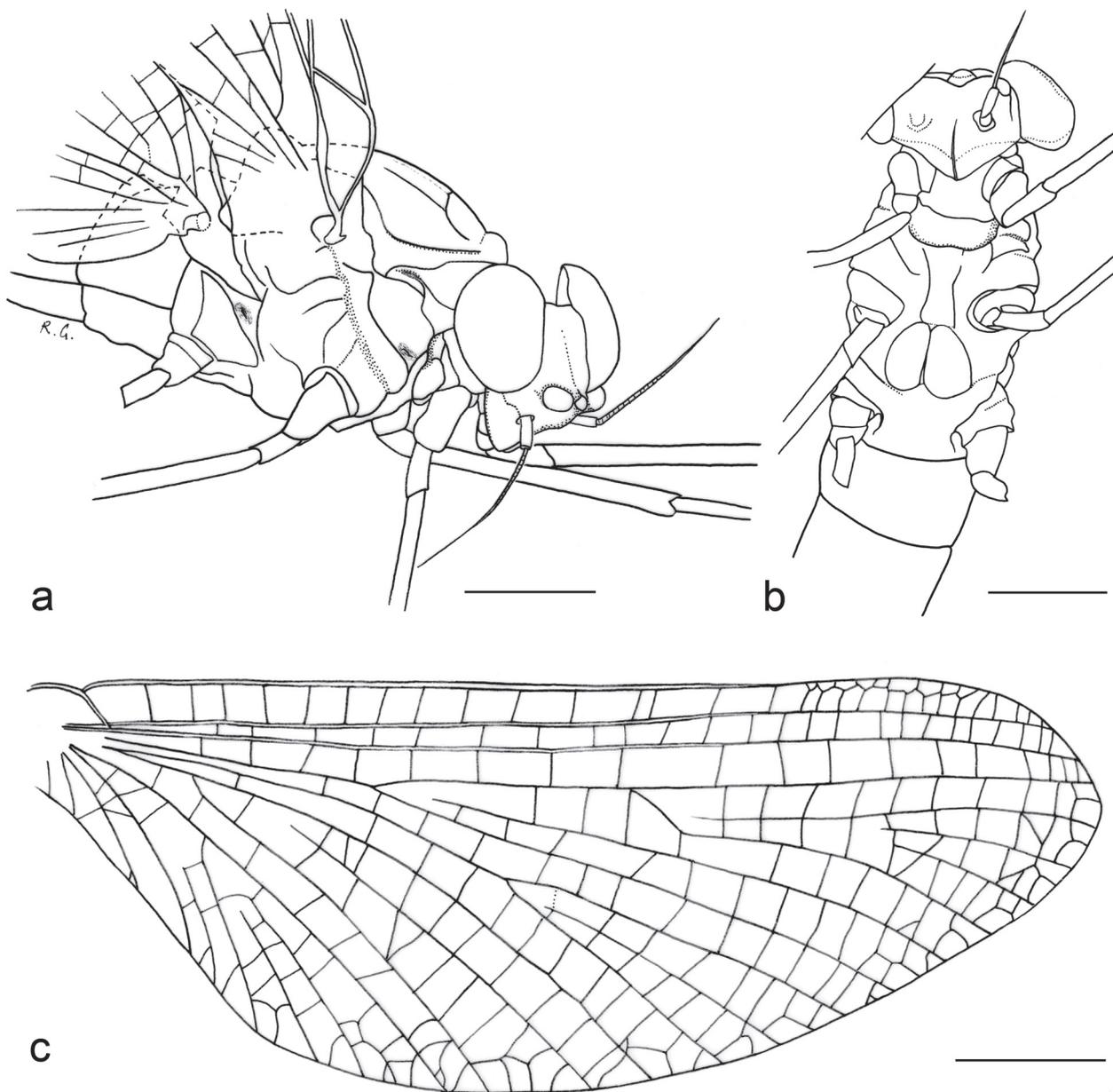


Fig. 4. *Siphloplecton barabani* sp. nov., holotype, female imago. – **a.** Head and thorax in lateral view. **b.** Head and thorax in ventral view. **c.** Right forewing. – Scale lines 1 mm.

fig. 15a, d). Subgenital plate relatively wide, 2.15× wide as long, convex and rounded apically. Subanal plate not elongate, narrow, pointed at the tip (Fig. 5d).

Paracercus is vestigial, comprising of 6 visible segments. Cerci well preserved.

Remarks. – This female specimen was initially described and designated as allotype of *S. macrops* by DEMOULIN (1968). As pointed out earlier, there is no reliable

character to place this female specimen within *S. macrops*, so it is formally described as new species herein.

Description of paratype. – Partly damaged specimen with visible anterior part of thorax, head, wings and legs, except of left hind wing and distal part of left forewing (Fig. 7a). For measurements see Tab. 2.

Colouration pale, yellow-brownish. Eyes, head, dorsal side of thorax darker than abdominal segments.

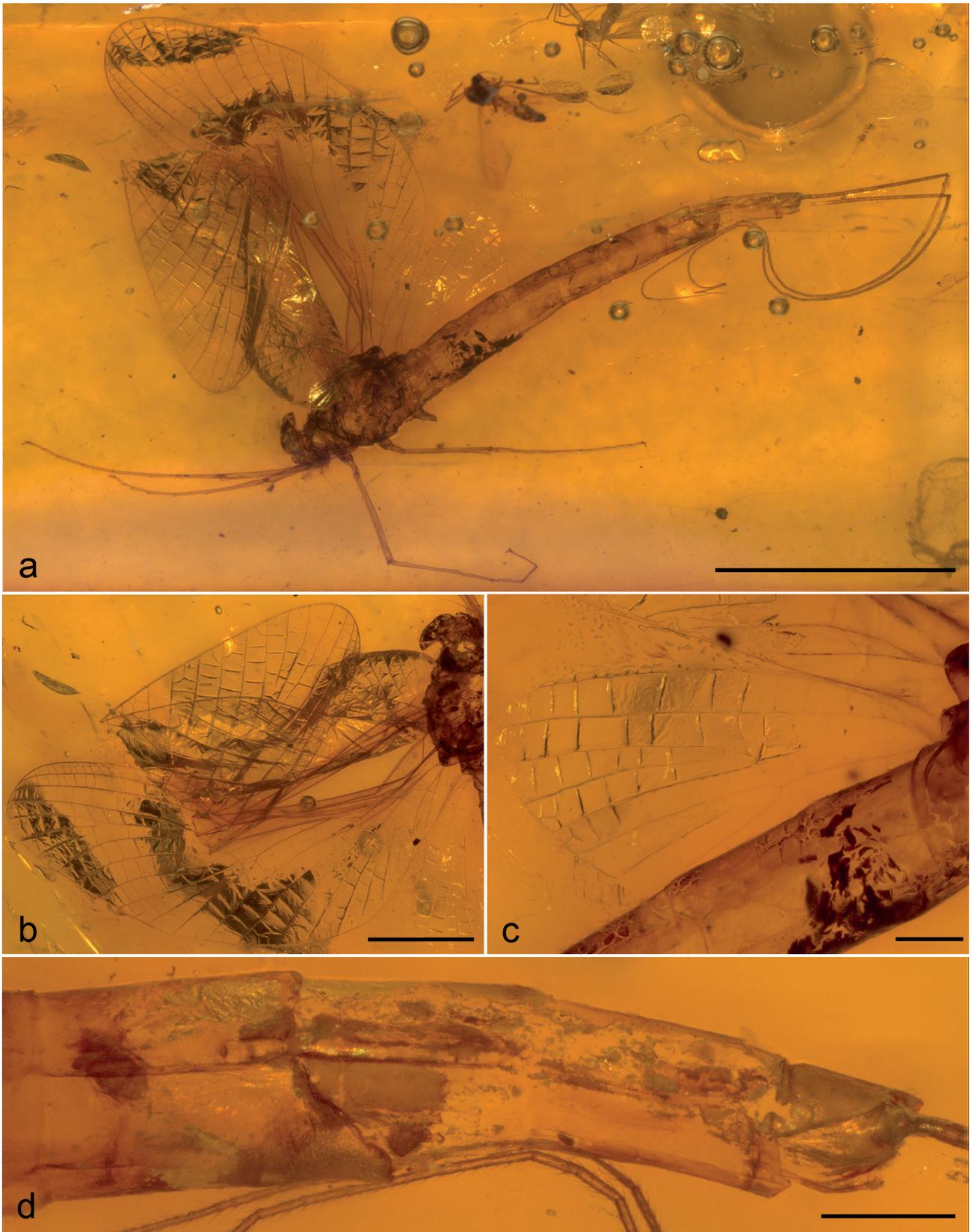


Fig. 5. *Siphloplecton barabani* sp. nov., holotype, female imago. – **a.** General lateral view. **b.** Forewings. **c.** Hind wing. **d.** Abdominal segments VII–X with subgenital and subanal plates. – Scale lines 5 mm (a), 2 mm (b), 0.5 mm (c, d).

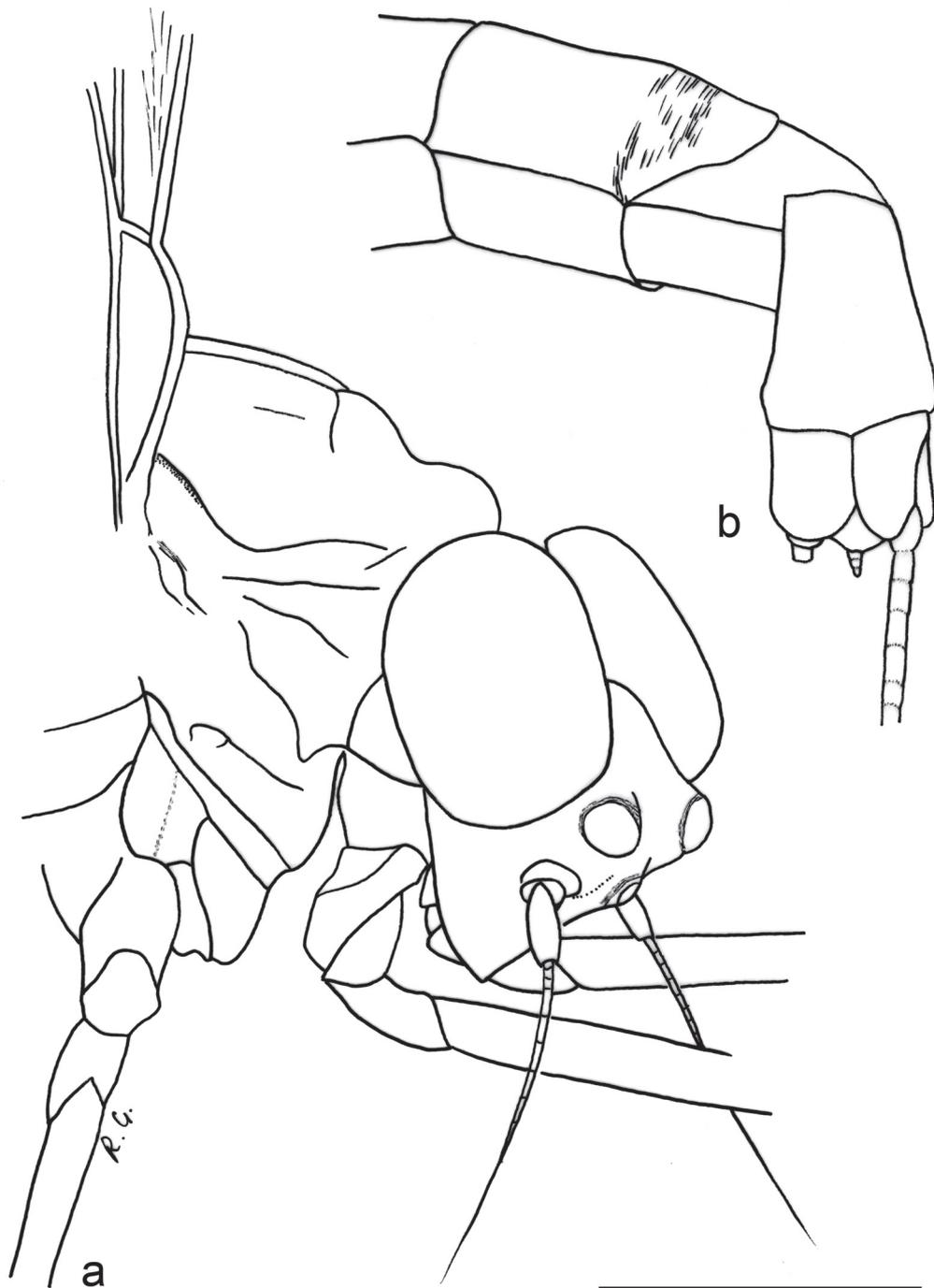


Fig. 6. *Siphloplecton barabani* sp. nov., paratype, female imago. – **a.** Head, pro- and anterior part of mesothorax in lateral view. **b.** Abdominal segments VII–X with subgenital and subanal plates. – Scale line 1 mm.

Lateroparapsidal suture hardly visible. In lateral aspect, mesonotal suture slightly stretched backward medially (Fig. 6a, see also KLUGE 2004, figs. 21D, 21E). Furcoster-nal protuberances contiguous (as in Fig. 4b).

Wings translucent, hyaline, not pigmented. Pterostigma with several anastomosed veins. Forewings with two pairs of intercalaries in cubital field typical of *Siphloplecton* (Fig. 7b). Right hind wing with small, bluntly pointed costal process (Fig. 7c).

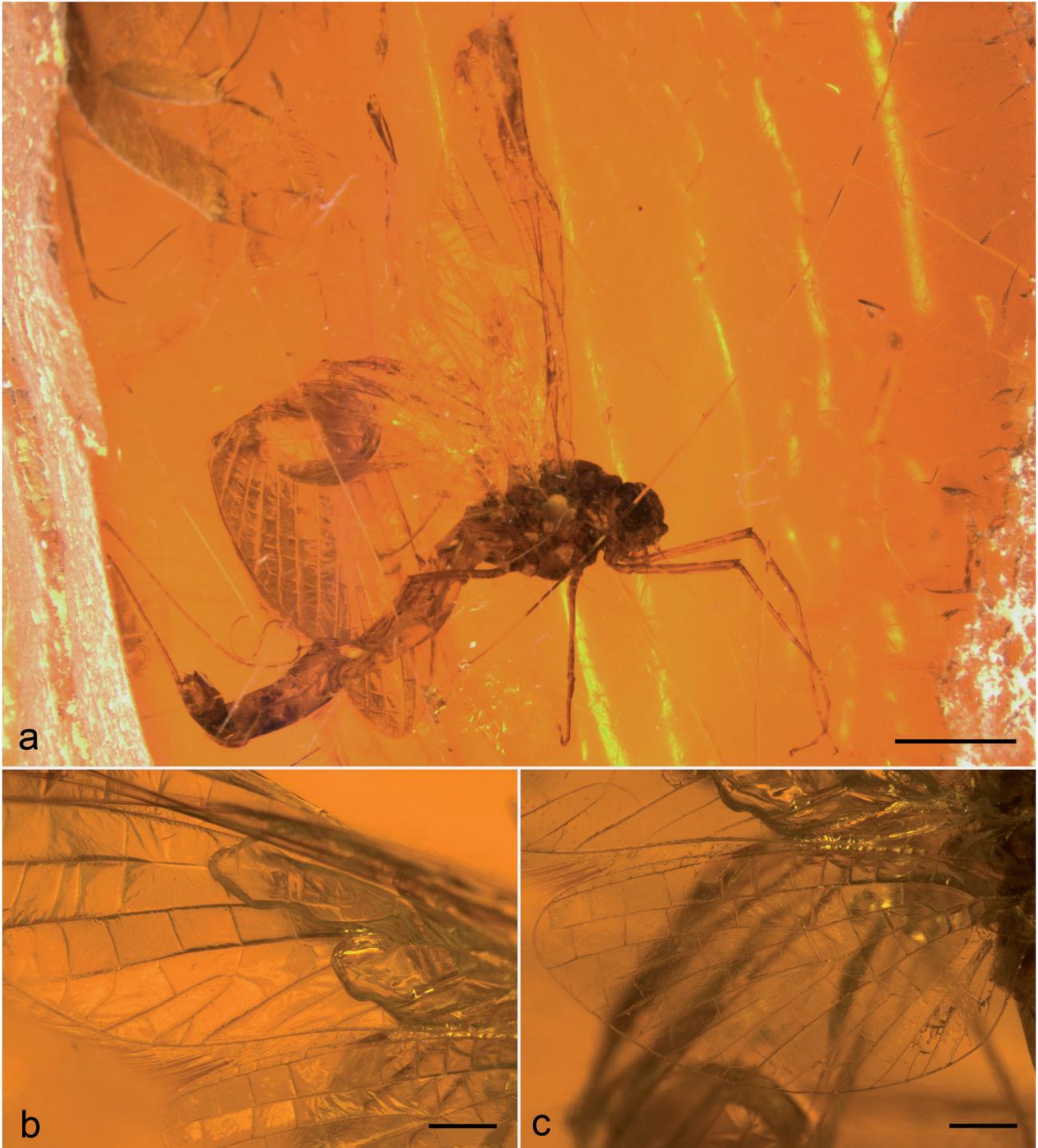


Fig. 7. *Siphloplecton barabani* sp. nov., paratype, female imago. – **a.** General lateral view. **b.** Cubital field of left forewing. **c.** Right hind wing in ventral view. – Scale lines 2 mm (a), 0.5 mm (b, c).

Measurements of leg segments in Tab. 2. First tarsal segments of middle and hind legs longest, fused with tibia. Tibia of middle legs with trace of tibiopatellar suture. Tarsi 5-segmented. All tarsal claws dissimilar.

Abdominal segments brownish, partly damaged. Subgenital plate convex and wide, with width/length ratio 2.07; subanal plate narrow with pointed tip (Fig. 6b). Cerci partly damaged. Paracercus with three visible segments.

Tab. 1. Measurements of *Siphloplecton barabani* sp. nov. (holotype, female imago).

Characters	(mm)
Length of body	10.55
Length of right foreleg	6.20
Length of femur	2.16
Length of tibia	1.52
Length of tarsus	2.52
Segment 1	0.76
Segment 2	0.68
Segment 3	0.46
Segment 4	0.38
Segment 5	0.38
Length of left foreleg	6.56
Length of femur	2.16
Length of tibia	1.56
Length of tarsus	2.84
Segment 1	0.78
Segment 2	0.76
Segment 3	0.50
Segment 4	0.40
Segment 5	0.40
Length of right middle leg	5.76
Length of femur	2.04
Length of tibia	1.36
Length of tarsus	2.36
Segment 1	0.72
Segment 2	0.60
Segment 3	0.44
Segment 4	0.28
Segment 5	0.32
Length of left middle leg	5.88
Length of femur	2.04
Length of tibia	1.40
Length of tarsus	2.44
Segment 1	0.72
Segment 2	0.64
Segment 3	0.44
Segment 4	0.32
Segment 5	0.32
Length of right hind leg	–
Length of femur	–
Length of tibia	–
Length of tarsus	–
Segment 1	–
Segment 2	–
Segment 3	–
Segment 4	–
Segment 5	–
Length of left hind leg	–
Length of femur	–
Length of tibia	–
Length of tarsus	–
Segment 1	–
Segment 2	–
Segment 3	–
Segment 4	–
Segment 5	–
Length of right forewing	–
Length of left forewing	7.09
Length of right hind wing	4.00
Length of left hind wing	–
Hind/forewings length ratio	0.56
Length of right cercus	22.72
Length of left cercus	23.72

Tab. 2. Measurements of *Siphloplecton barabani* sp. nov. (paratype, female imago). * = preserved part.

Characters	(mm)
Length of body	10.32
Length of right foreleg	6.00
Length of femur	1.92
Length of tibia	1.68
Length of tarsus	2.40
Segment 1	0.68
Segment 2	0.56
Segment 3	0.48
Segment 4	0.40
Segment 5	0.28
Length of left foreleg	6.08
Length of femur	2.00
Length of tibia	1.72
Length of tarsus	2.36
Segment 1	0.68
Segment 2	0.56
Segment 3	0.48
Segment 4	0.40
Segment 5	0.24
Length of right middle leg	4.68*
Length of femur	1.64
Length of tibia	1.04
Length of tarsus	2.00*
Segment 1	0.40
Segment 2	0.48
Segment 3	0.44
Segment 4	0.28*
Segment 5	0.40
Length of left middle leg	4.40*
Length of femur	1.64
Length of tibia	0.96
Length of tarsus	1.80*
Segment 1	0.44
Segment 2	0.48
Segment 3	0.48
Segment 4	0.40
Segment 5	–
Length of right hind leg	4.44*
Length of femur	1.72
Length of tibia	1.08
Length of tarsus	1.64*
Segment 1	0.32*
Segment 2	0.44
Segment 3	0.36
Segment 4	0.28
Segment 5	0.24
Length of left hind leg	4.24*
Length of femur	1.60*
Length of tibia	0.96*
Length of tarsus	1.68*
Segment 1	0.32*
Segment 2	0.44
Segment 3	0.40
Segment 4	0.28
Segment 5	0.24
Length of right forewing	10.60*
Length of left forewing	10.76*
Length of right hind wing	3.40*
Length of left hind wing	3.88
Hind/forewings length ratio	0.35*
Length of cercus (only one is preserved)	12.40*

Remarks. – This female specimen was initially described and assigned to *S. jaegeri* by DEMOULIN (1970). It can be attributed to *Siphloplecton barabani* sp. nov. by the structure of subanal and subgenital plates resembling the ones of holotype. Some differences are present in measurements of leg segments.

Discussion. – For discriminating characters of *S. barabani* sp. nov. see Discussion in 3.1.1.4.

3.1.1.4. *Siphloplecton hageni* sp. nov.

(fig. 16 in DEMOULIN 1968)

Figs. 8, 9; Tab. 3

1968 *Siphloplecton macrops* (PICTET, 1856) [in partim]. – DEMOULIN, p. 249, fig. 16 (description).
For remaining synonymies see 3.1.1.1.

Holotype: Female imago, DEMOULIN (1968: 252, fig. 16), originally labeled: “Fam. Ephemeridae 9” “G. DEMOULIN det., 1966 *Siphloplecton macrops* (Pictet) ♀ imago Demoulin, F. 16”. SIMON collection, MNB MB.I.2237 (Figs. 8, 9).

Stratum typicum: Eocene, Baltic amber.

Etymology: Named in honour of German entomologist HERMANN AUGUST HAGEN.

Description of holotype. – Well preserved female imago. For measurements see Tab. 3. General colour of body pale, yellow-brown. Eyes medially well separated.

Dorsal side of thorax well visible. Lateroparapsidal suture is elongate. Mesonotal suture nearly transverse (Fig. 8a). Furcasternal protuberances of mesothorax are contiguous (Fig. 8b).

Wings translucent, hyaline, not pigmented. Basal part of right forewing with milky, large spots of “Verlummung”. For this reason, except of the costal, subcostal, and RA field, details of forewing venation invisible. Venation of right hind wing also not visible. Left fore- and hind wings completely preserved but arcuated and twisted (Figs. 9a–c). Pterostigma with several anastomosed cross veins. Two pairs of cubital intercalaries present in left forewing. Hind wings 0.35× of forewing length, with three pairs of triads. Costal process bluntly pointed and small.

Legs well preserved except left hind leg. Measurements of legs segments in Tab. 3. First tarsal segments of middle and hind legs fused with tibia. Tibia of middle and hind legs with traces of tibiopatellar suture. Tarsi 5-segmented. Tarsal claws dissimilar with one hooked and one blunt claw.

Abdominal segments completely preserved. Subanal and subgenital plates (Fig. 9d) also figured by DEMOULIN (1968: 251, fig. 16a, b). Subgenital plate elongated, 1.57× as wide as long, rounded apically. Subanal plate relatively broad, triangular with obtuse tip. Paracercus vestigial, at least 4-segmented. Cerci not preserved.

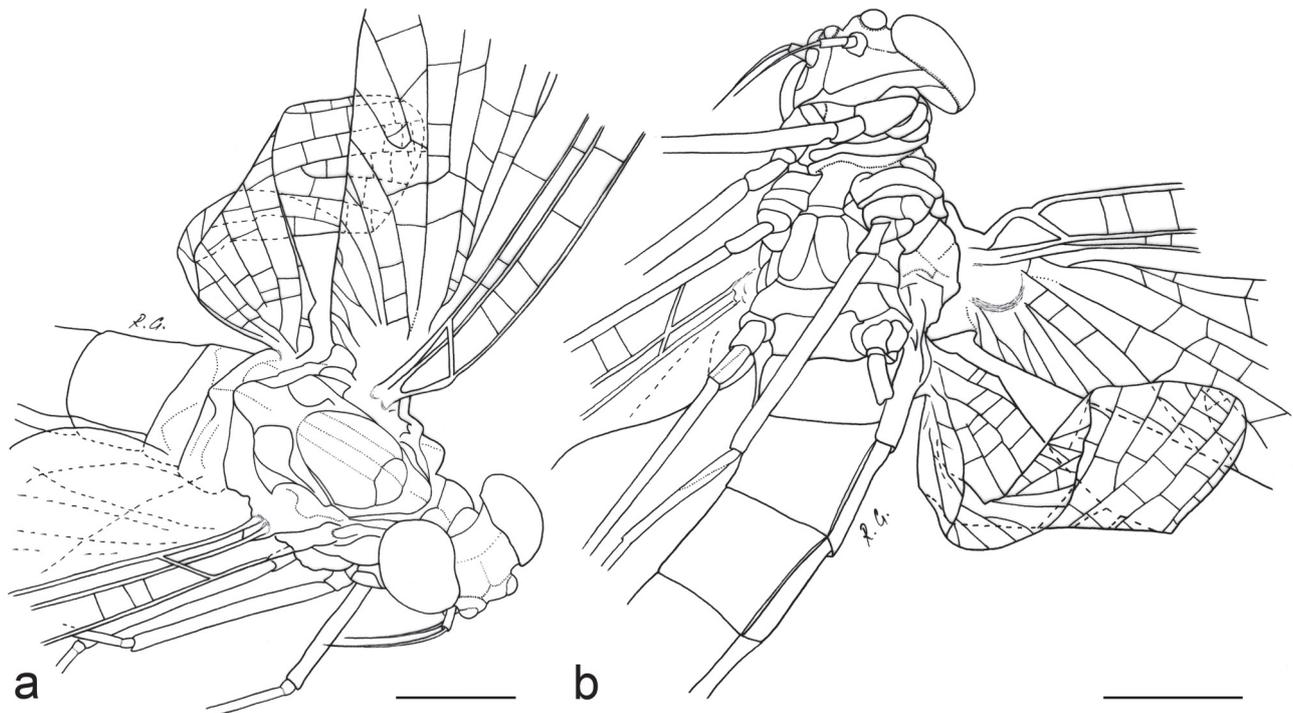


Fig. 8. *Siphloplecton hageni* sp. nov., holotype, female imago. – a. Head, thorax, wing base and first abdominal segments in dorsal view. b. Head, thorax, wing base and first abdominal segments in ventral view. – Scale lines 1 mm.

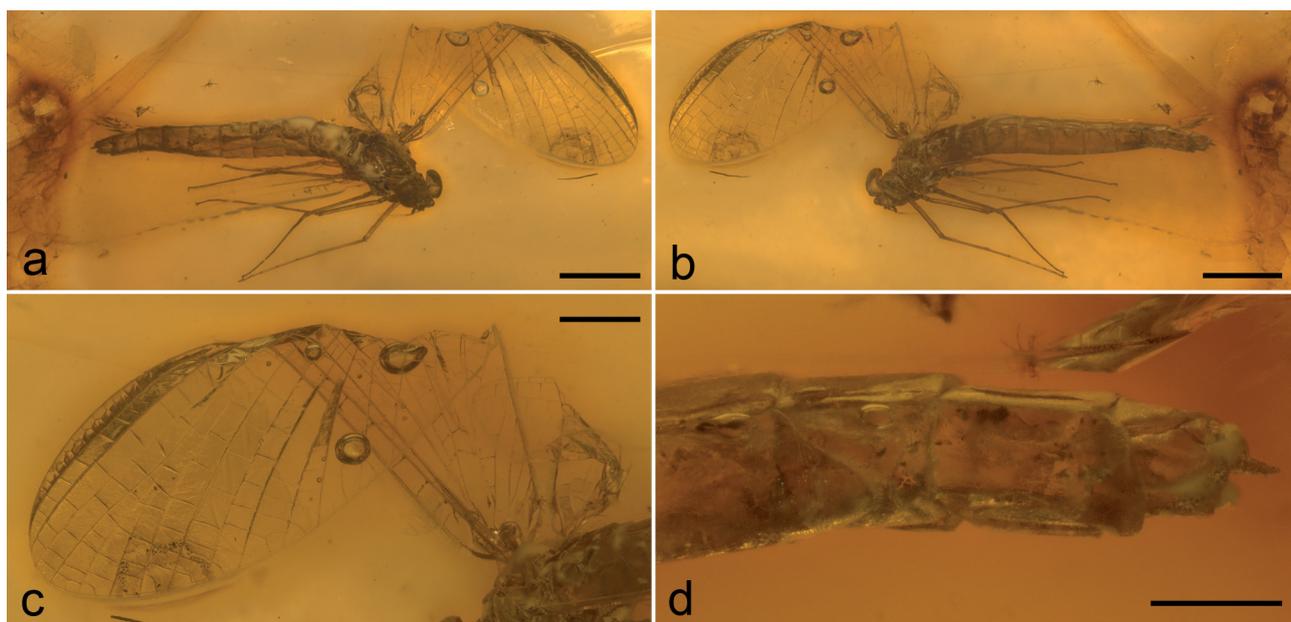


Fig. 9. *Siphloplecton hageni* sp. nov., holotype, female imago. – **a.** General dorsal view. **b.** General ventral view. **c.** Left forewing. **d.** Abdominal segments VII–X with subgenital and subanal plates. – Scale lines 2 mm (a, b), 1 mm (c), 0.5 mm (d).

Tab. 3. Measurements of *Siphloplecton hageni* sp. nov. (holotype, female imago).

Characters	(mm)		
Length of body	9.68	Length of tibia	1.02
Length of right foreleg	5.27	Length of tarsus	1.79
Length of femur	1.70	Segment 1	0.55
Length of tibia	1.25	Segment 2	0.45
Length of tarsus	2.32	Segment 3	0.35
Segment 1	0.60	Segment 4	0.22
Segment 2	0.55	Segment 5	0.22
Segment 3	0.47	Length of right hind leg	3.86
Segment 4	0.35	Length of femur	1.62
Segment 5	0.35	Length of tibia	0.87
Length of left foreleg	5.36	Length of tarsus	1.37
Length of femur	1.70	Segment 1	0.45
Length of tibia	1.32	Segment 2	0.35
Length of tarsus	2.34	Segment 3	0.27
Segment 1	0.57	Segment 4	0.15
Segment 2	0.57	Segment 5	0.15
Segment 3	0.50	Length of left hind leg	–
Segment 4	0.35	Length of femur	–
Segment 5	0.35	Length of tibia	–
Length of right middle leg	4.40	Length of tarsus	–
Length of femur	1.67	Segment 1	–
Length of tibia	1.02	Segment 2	–
Length of tarsus	1.71	Segment 3	–
Segment 1	0.55	Segment 4	–
Segment 2	0.37	Segment 5	–
Segment 3	0.32	Length of right forewing	10.00
Segment 4	0.25	Length of left forewing	10.00
Segment 5	0.22	Length of right hind wing	–
Length of left middle leg	4.53	Length of left hind wing	3.52
Length of femur	1.72	Hind/forewings length ratio	0.35
		Length of cerci	–

Discussion. – *Siphloplecton barabani* sp. nov. and *Siphloplecton hageni* sp. nov. can be clearly attributed to the genus *Siphloplecton* by the presence of (1) elongate lateroparapsidal suture; (2) mesonotal suture stretched backward medially or nearly transverse; (3) pairs of two intercalaries of cubital field of forewings; (4) vestigial paracercus.

An assignment of described fossil females to one of the two extant species groups (see BERNER 1978) is impossible, since no traces of wing pigmentation are preserved. However, it cannot be excluded that all fossil representatives of *Siphloplecton* are lacking wing pigmentation similar as seen in the Recent species *S. speciosum*.

Siphloplecton barabani sp. nov. is distinguished from *Siphloplecton hageni* sp. nov. by its medially slightly bulged mesonotal suture (in contrast to the nearly transverse mesonotal suture in *Siphloplecton hageni* sp. nov.), shape and proportions of the relatively wide subgenital plate with width/length ratio 2.15 (in contrast to the elongate subgenital plate of *Siphloplecton hageni* sp. nov. with a ratio of 1.57), and shape of subanal plate that is not elongate, narrow and apically pointed (in contrast to a relatively broad and triangular subanal plate with obtuse tip in *Siphloplecton hageni* sp. nov.).

Some differences are also present in body size, wing and leg proportions (see Tab. 3).

3.1.1.5. *Siphloplecton jaegeri* DEMOULIN, 1968
(fig. 18a, c in DEMOULIN 1968)
Figs. 10, 11; Tab. 4

- 1968 *Siphloplecton jaegeri* DEMOULIN, 1968. – DEMOULIN, p. 252 (description, designation of holotype); nec DEMOULIN (1970, p. 3, figs. 3a, b).
1987 *Siphloplecton jaegeri* DEMOULIN [in partim]. – HUBBARD, p. 46 (list of synonymy).
1998 *Siphloplecton jaegeri* DEMOULIN, 1968. – WEITSCHAT & WICHARD, p. 94 (species list).
2009 *Siphloplecton jaegeri* DEMOULIN, 1968. – WICHARD et al., p. 291 (species list).

Holotype: Male imago, DEMOULIN (1968: 252, fig. 18a, b), originally labeled: “Holotype 2 Fam. Ephemeroidea Orig am DEMOULIN 1968, Fig. 18”; “G. DEMOULIN, 1966 *Siphloplecton jaegeri* sp. n. ♂ imago”. SIMON collection, MNB, MB.I.2242 (Figs. 10, 11).

Stratum typicum: Eocene, Baltic amber.

Description of holotype. – Damaged specimen without head, visible in dorsal and ventral aspect. For measurements see Tab. 4.

General colouration pale, yellowish brown to brown. Colouration of dorsal side slightly darker than ventral side.

Right side of thorax invisible through influxes of resin. Left side of thorax with “Verlumpung” and partly damaged. Dorsal side of thorax typical of *Siphloplecton* with elon-

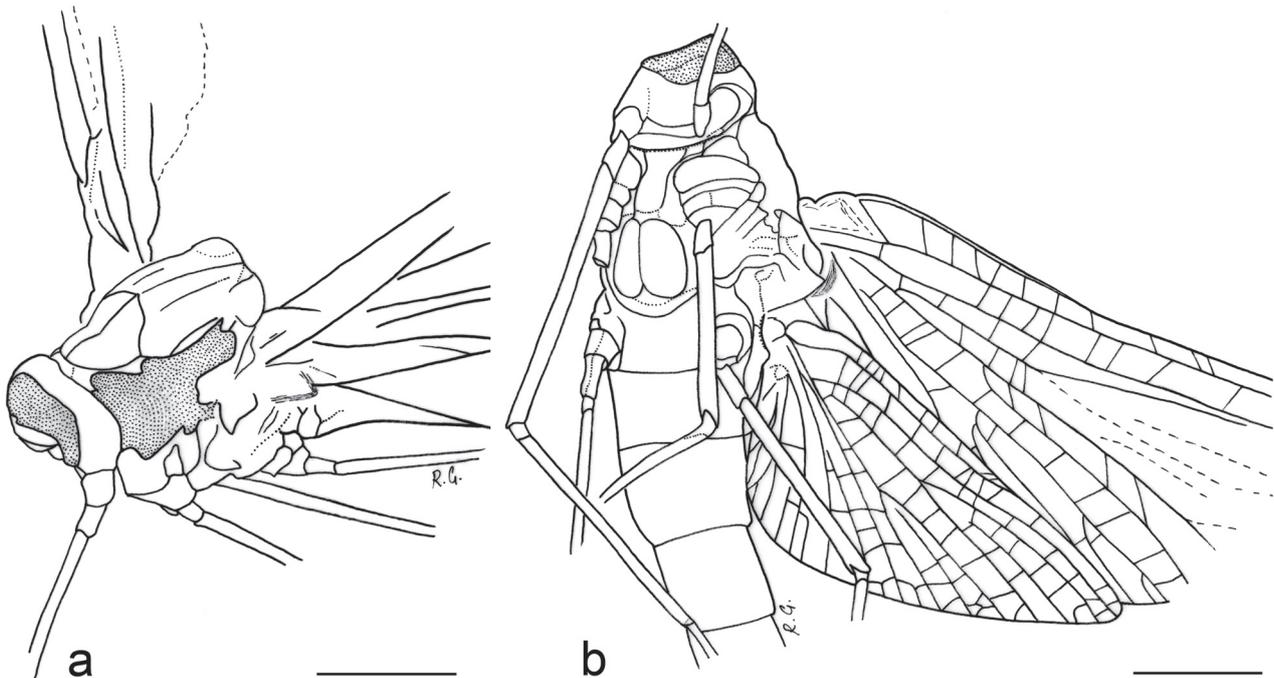


Fig. 10. *Siphloplecton jaegeri* DEMOULIN, 1968, holotype, male imago. – a. Thorax in dorsolateral view. b. Thorax, wings and first abdominal segments in ventral view. – Scale lines 1 mm.

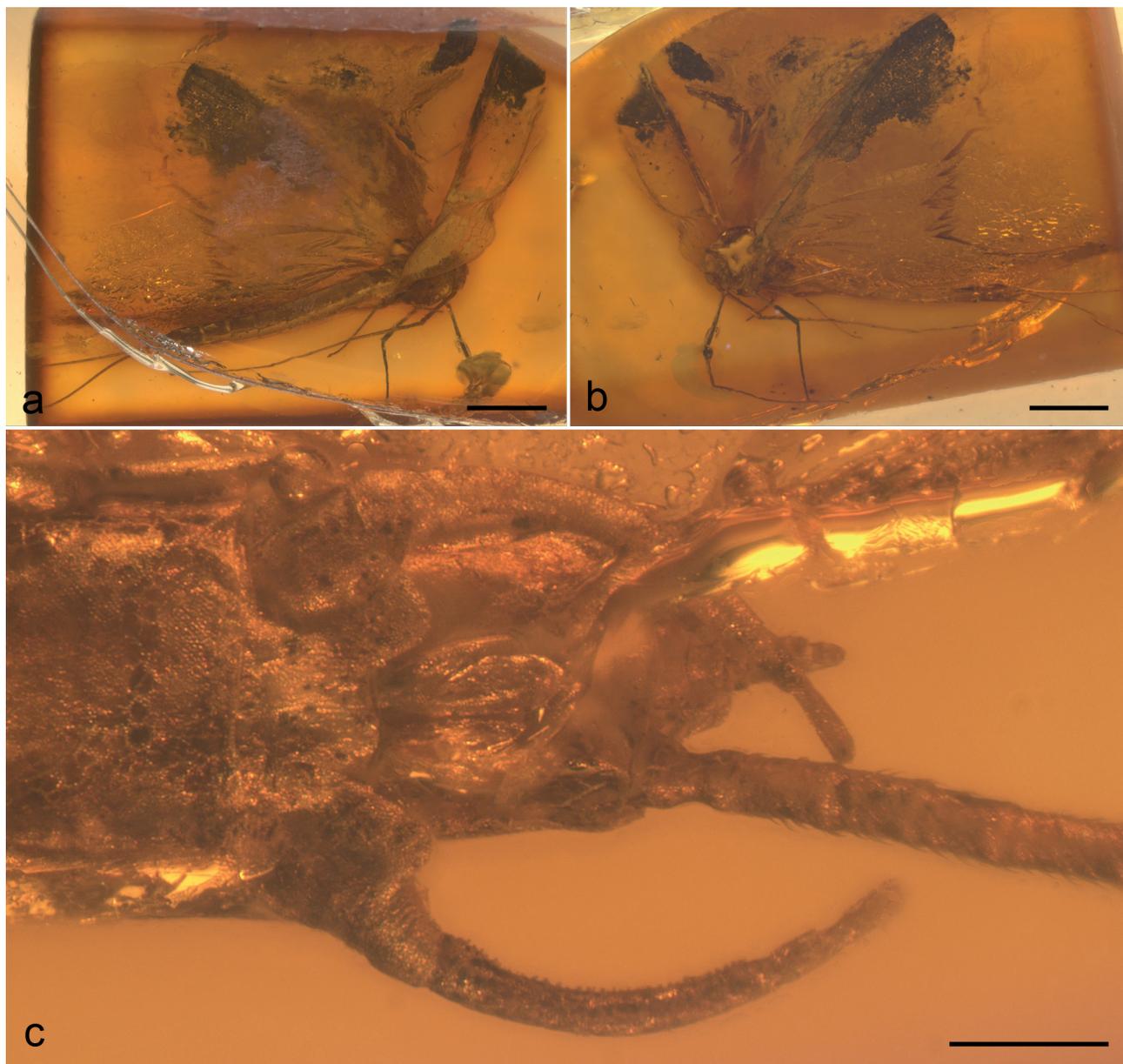


Fig. 11. *Siphloplecton jaegeri* DEMOULIN, 1968, holotype, male imago. – **a.** General dorsal view. **b.** General ventral view. **c.** male genitalia in ventral view. – Scale lines 2 mm (a, b), 0.2 mm (c).

gate lateroparapsidal suture (pigmentation around LPs not preserved); mesonotal suture stretched backward medially (Fig. 10a); furcasternal protuberances of mesothorax contiguous (Fig. 10b).

Wings hyaline, transparent. Pterostigmatic area with several anastomosed veins. Right forewing twisted, apical part is lost. Only cubital field of left forewing well preserved, presenting one pair of intercalaries apically connected to each other and directed towards CuA, plus one additional distal intercalary vein connected with CuA (Fig. 10b). Hind wings impregnated with resin, covered by

forewings, hardly visible because superimposed by cubital field of forewings. Hind wings with triads RS, MA and MP, preserved part of hind wing $0.49\times$ forewing length. Costal process relatively blunt and small.

Legs well preserved. First tarsal segment of middle and hind leg longest, fused with tibia. Outer margin of foretibia with pointed spines. Trace of tibiopatellar suture present in middle and hind legs. Tarsi 5-segmented. Tarsal claws dissimilar (one claw hooked, other one blunt) (see DEMOULIN 1968, fig. 18b).

Abdominal segments well preserved.

Tab. 4. Measurements of *Siphloplecton jaegeri* DEMOULIN, 1968 (holotype, male imago). * = preserved part.

Characters	(mm)
Length of body	9.00*
Length of right foreleg	8.16*
Length of femur	1.30*
Length of tibia	2.00
Length of tarsus	4.86
Segment 1	1.07
Segment 2	1.07
Segment 3	1.02
Segment 4	1.02
Segment 5	0.68
Length of left foreleg	8.58
Length of femur	1.75
Length of tibia	2.05
Length of tarsus	4.78
Segment 1	1.07
Segment 2	1.05
Segment 3	1.02
Segment 4	1.00
Segment 5	0.64
Length of right middle leg	2.49*
Length of femur	1.37
Length of tibia	1.12*
Length of tarsus	–
Segment 1	–
Segment 2	–
Segment 3	–
Segment 4	–
Segment 5	–
Length of left middle leg	2.81*
Length of femur	1.32
Length of tibia	1.17*
Length of tarsus	0.32*
Segment 1	0.32*
Segment 2	–
Segment 3	–
Segment 4	–
Segment 5	–
Length of right hind leg	3.19
Length of femur	1.30
Length of tibia	0.70
Length of tarsus	1.19
Segment 1	0.35
Segment 2	0.32
Segment 3	0.22
Segment 4	0.10
Segment 5	0.20
Length of left hind leg	3.18
Length of femur	1.35
Length of tibia	0.70
Length of tarsus	1.13
Segment 1	0.37
Segment 2	0.32
Segment 3	0.17
Segment 4	0.12
Segment 5	0.15
Length of right forewing	7.00*
Length of left forewing	7.76*
Length of right hind wing	3.60
Length of left hind wing	3.72
Hind/forewings length ratio	0.49*
Length of right cercus	3.60*
Length of left cercus	4.40*

Styliger plate angulate, medioapically deeply incised; incision with pronounced, broad, triangular projection. Medially of each gonostylus, lateral parts of styliger plate triangular and broadly protruding. Basal segment of forceps basally markedly narrower than adjoining apical part of styliger plate; forceps 4-segmented, segment 4 approximately 2.83× as long as wide (Fig. 11c).

Penis lobes distinctly elongated, medially incised, apically of triangular shape. Penis lobes only with inconspicuous incision between lateral and medial penis sclerite. Surface of penis lobes not visible.

Paracercus vestigial, at least 3-segmented. Cerci partly lost.

Discussion. – *S. jaegeri* occupies a relatively isolated position within fossil and Recent species of *Siphloplecton*. From all other representatives of the genus, this species can be separated by (1) presence of only three intercalary veins in cubital field of forewing which are grouping in one pair connected apically with CuA and one additional small intercalary vein near CuA; (2) absence of spines on outer side of foretibia; (3) shape of deeply incised styliger plate with markedly broad lateral and medial projections; (4) distinctly elongate penis lobes with triangular shape apically.

3.1.1.6. *Siphloplecton demoulini* sp. nov.

(fig. 3a, b in DEMOULIN 1970)

Figs. 12, 13, Tab. 5

1970 *Siphloplecton jaegeri* DEMOULIN, 1968 [in partim]. – DEMOULIN, p. 3, figs. 3a, b (description); nec DEMOULIN, 1968 (252, fig. 18a, b).

Holotype: Male imago, DEMOULIN (1970: 252, fig. 3a, b), originally labeled: “G. DEMOULIN det., 1968 *Siphloplecton jaegeri* DEMOULIN ♂”; “4672 Éphémère”. BURSEY collection, MNHN, Nr 4672. Label of slide preparation: “4672 Ephemeroptera *Siphloplecton jaegeri* ♂ DEMOULIN” (Figs. 12, 13).

Stratum typicum: Eocene, Baltic amber.

Etymology: Named in honour of Belgian entomologist GEORGES DEMOULIN.

Description of holotype. – Male imago, separated into two parts, preserved in two pieces of amber: one piece with body, wings, head and legs (Fig. 12a) mounted on slide and embedded in resin, second piece in original amber with part of cercus. Well preserved specimen, visible in dorsoventral aspect. For measurements see Tab. 5.

General colouration pale. Colouration of ventral side of head darker than dorsal side. Ocelli broad without traces of pigmentation. Eyes broad, medially contiguous.

Thorax with elongate lateroparapsidal suture, without any traces of pigmentation around lateroparapsidal suture; mesonotal suture bulged medially (Fig. 12a); furcasternal protuberances of mesothorax contiguous (Fig. 12b). Pigmentation of thoracic terga not preserved.

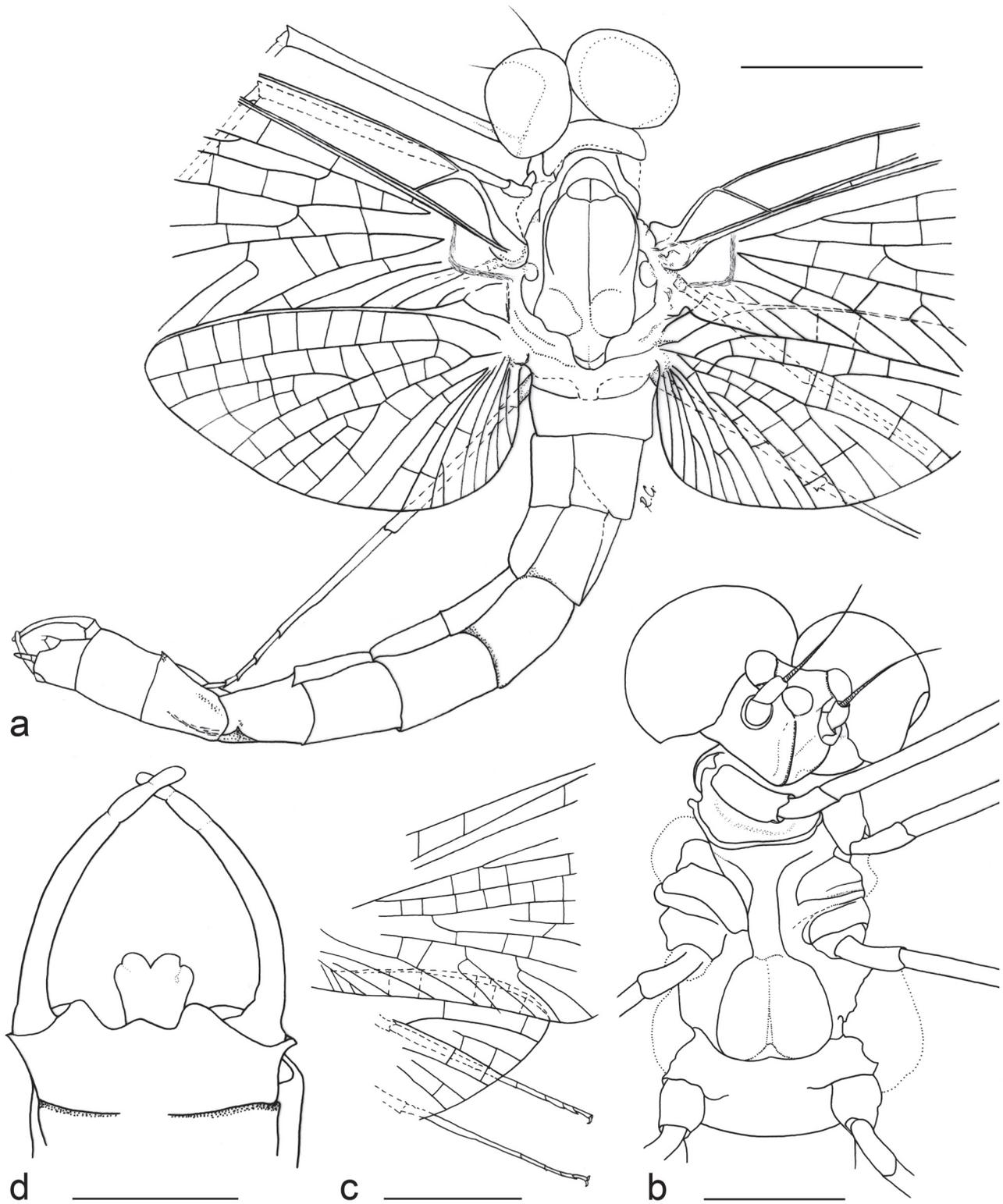


Fig. 12. *Siphloplecton demoulini*, sp. nov., holotype, male imago. – **a.** General dorsal view. **b.** Head and thorax in ventral view. **c.** Cubital field of right forewing in dorsal view. **d.** Male genitalia in ventral view. – Scale lines 2 mm (a, c), 1 mm (b), 0.5 mm (d).

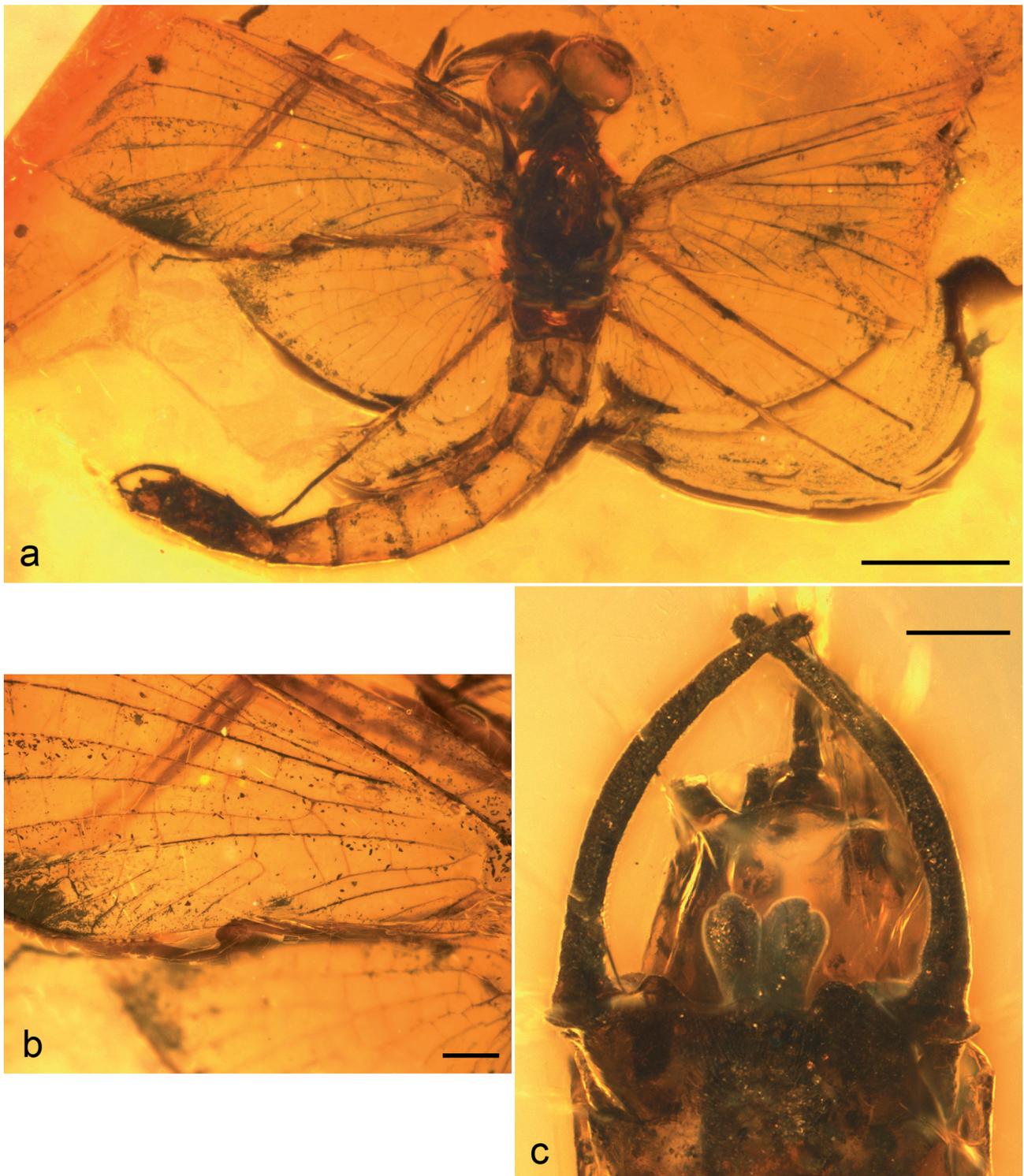


Fig. 13. *Siphloplecton demoulini*, sp. nov., holotype, male imago. – **a.** General dorsal view. **b.** Cubital field of left forewing in dorsal view. **c.** Male genitalia in ventral view. – Scale lines 2 mm (a), 0.5 mm (b), 0.2 mm (c).

Tab. 5. Measurements of *Siphloplecton demoulini* sp. nov. (holotype, male imago). * = preserved part.

Characters	(mm)
Length of body	11.20
Length of right foreleg	10.60*
Length of femur	3.00
Length of tibia	2.80
Length of tarsus	4.80*
Segment 1	1.68
Segment 2	1.72
Segment 3	1.40*
Segment 4	–
Segment 5	–
Length of left foreleg	10.44*
Length of femur	3.00
Length of tibia	2.80
Length of tarsus	4.64*
Segment 1	1.60
Segment 2	1.72
Segment 3	1.32*
Segment 4	–
Segment 5	–
Length of right middle leg	5.08
Length of femur	1.88
Length of tibia	1.32
Length of tarsus	1.88
Segment 1	0.60
Segment 2	0.48
Segment 3	0.32
Segment 4	0.24
Segment 5	0.24
Length of left middle leg	5.00
Length of femur	1.80
Length of tibia	1.28
Length of tarsus	1.92
Segment 1	0.56
Segment 2	0.48
Segment 3	0.32
Segment 4	0.28
Segment 5	0.28
Length of right hind leg	4.88
Length of femur	1.88
Length of tibia	1.28
Length of tarsus	1.72
Segment 1	0.56
Segment 2	0.40
Segment 3	0.28
Segment 4	0.24
Segment 5	0.24
Length of left hind leg	4.60
Length of femur	1.84
Length of tibia	1.08
Length of tarsus	1.68
Segment 1	0.56
Segment 2	0.40
Segment 3	0.28
Segment 4	0.20
Segment 5	0.24
Length of right forewing	10.68
Length of left forewing	3.84
Length of right hind wing	10.40
Length of left hind wing	3.92
Hind/forewings length ratio	0.37
Length of cercus (only one is preserved)	21.00*

Wings translucent, hyaline, not pigmented, distally damaged. Pterostigmatic area not preserved. Cubital field of forewings with two pairs of intercalaries (Fig. 12c). Hind wings with triads RS, MA and MP, 0.37× forewing length. Costal process of hind wing bluntly pointed (Fig. 12a).

Legs well preserved, except of left middle leg. First tarsal segment of middle and hind leg longest, fused with tibia. Tibia of foreleg without spines on outer margin. Tibia of middle and hind legs with trace of tibiopatellar suture. Tarsi 5-segmented. Tarsal claws dissimilar with one hooked and one blunt claw.

Abdominal segments completely preserved. Styliiger plate angulate, mediocaudally incised; incision with relatively pronounced, triangular projection; incision medially to each gonostylus bordered by lateral, triangular projection. Basal segment of forceps basally narrower than adjoining apical part of the styliiger plate; forceps 4-segmented, segment 4 approximately 3.0× longer than wide (Fig. 12d). Penis lobes elongated, rounded at tips, markedly expanding laterally. Median and lateral sclerites rounded and separated by distinct incision. Penis lobes medially contiguous at almost entire length (Fig. 12d). Surface of penis lobes invisible.

Paracercus vestigial, at least 3-segmented. Cerci lost.

Discussion. – DEMOULIN (1970) assigned this specimen to *S. jaegeri* based on shape of penis lobes and styliiger plate. At the same time, he stated that the body size of the *S. jaegeri* specimen from MNHN (see 3.1.1.5.) is considerably larger than in this specimen.

This specimen is placed as *Siphloplecton demoulini* sp. nov. within the *S. basale* species group by the combination of several characters: (1) two pairs of intercalaries present in cubital field of forewing (the same in all fossil and recent species of the genus); (2) spines on outer margin of foretibia absent (in contrast to all Recent species); (3) styliiger plate with relatively broad lateral projections (in contrast to Recent species and to *S. picteti*); (4) penis lobes elongated and medially only apically incised (in contrast to *S. picteti* and Recent representatives of *S. interlineatum* species group), with median and lateral sclerites of penis lobe rounded and separated by distinct incision (in contrast to *S. jaegeri*).

3.1.1.7. *Siphloplecton* spp.

In his contributions to *S. macrops* and *S. jaegeri*, DEMOULIN (1968, 1970) assigned four other fossil specimens to *Siphloplecton* sp. While all of these specimens can indeed be attributed to the genus *Siphloplecton*, their poor state of preservation without visible genitalia do not allow a closer assignment within the genus nor an attribution to species level.

3.1.1.7.1. *Siphloplecton* sp. 1
(fig. 17a in DEMOULIN 1968)
Fig. 14

1968 *Siphloplecton macrops* (PICTET, 1856). – DEMOULIN, p. 249
(description), fig. 17a; nec PICTET-BARABAN & HAGEN
(1856).

For remaining synonymies see 3.1.1.1.

Material: Female imago, DEMOULIN (1968: 252, fig. 17a),
STANTIEN & BECKER collection, GZG (Fig. 14).

Stratum typicum: Eocene, Baltic amber.

Description. – Generally well preserved specimen with body, legs and wings visible in dorsal and ventral aspect, but with damaged left forewing and without preserved terminal filaments, tip of abdomen and genitalia not well visible because of “Verlumpung” (Fig. 14).

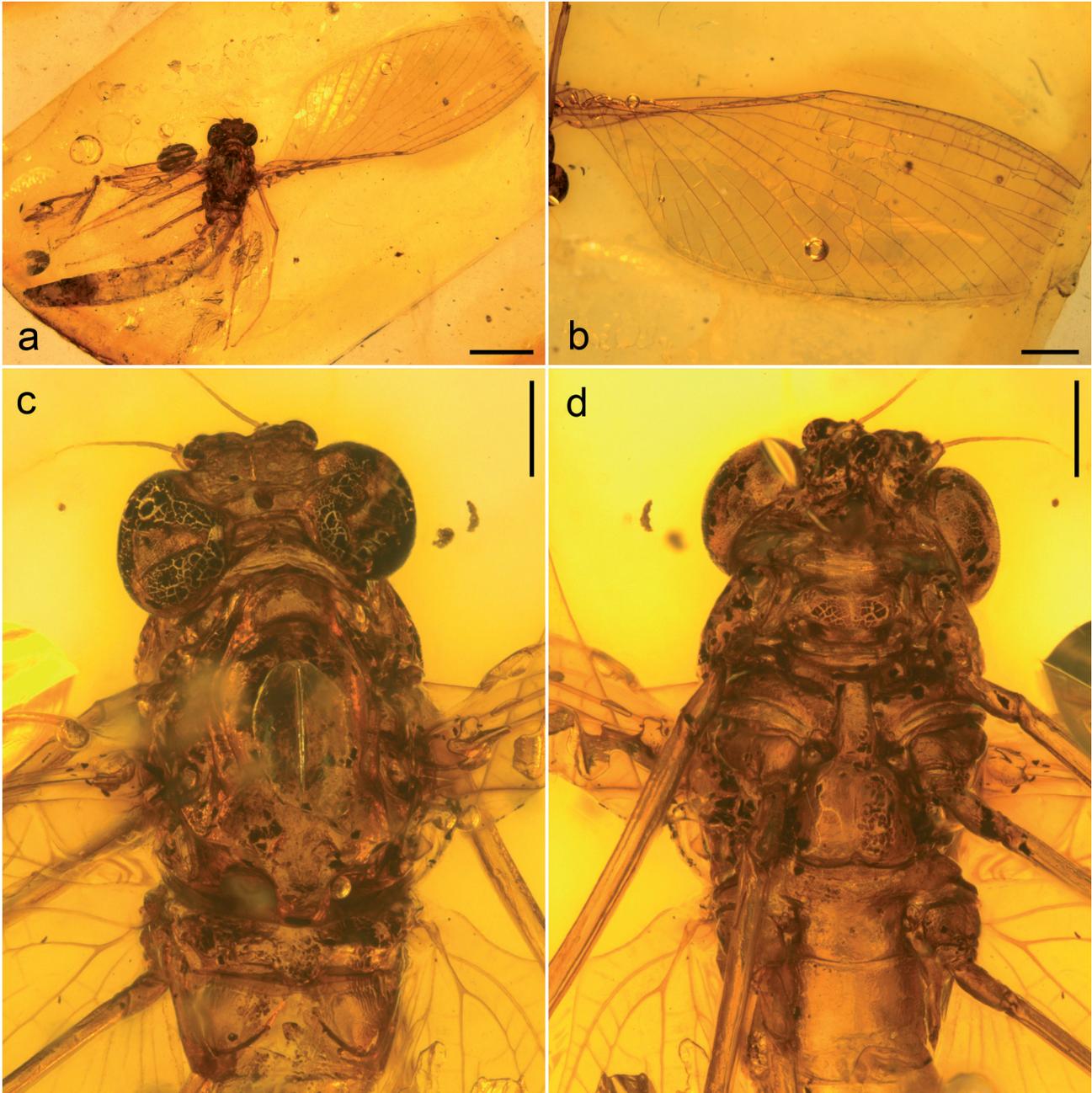


Fig. 14. *Siphloplecton* sp. 1, female imago. – a. General dorsal view. b. Right forewing in ventral view. c. Head and thorax in dorsal view. d. Head and thorax in ventral view. – Scale lines 2 mm (a), 1 mm (b), 0.5 mm (c, d).

3.1.1.7.2. *Siphloplecton* sp. 2
(fig. 17b in DEMOULIN 1968)

1968 *Siphloplecton macrops* (P ICTET, 1856). – DEMOULIN, p. 249, fig. 17b (description); nec P ICTET-BARABAN & HAGEN (1856).

For remaining synonymies see 3.1.1.1.

Material: Female imago, DEMOULIN (1968: 252, fig. 17b). STANTIEN & BECKER collection, GZG.

Stratum typicum: Eocene, Baltic amber.

Description. – DEMOULIN (1968) figured this female specimen with significant amount of “Verlummung” on head, thorax, and basal parts of right forewing. It appeared to have a damaged apical part of right forewing and damaged legs, only left pair of wings and abdomen seemed to be entirely preserved. It was embedded in a lateral position, but DEMOULIN neither described the female subgenital or subanal plate nor figured these characters in detail.

Remarks. – This specimen also belonged to the STANTIEN & BECKER collection, but it could not be anymore

located in the GZG where this collection is housed today, so the specimen appears to be lost. As there is no reinvestigation possible, this specimen cannot be assigned to a certain species.

3.1.1.7.3. *Siphloplecton* sp. 3
(fig. 19 in DEMOULIN 1968)

1968 *Siphloplecton* sp. – DEMOULIN, p. 254, fig. 19 (description).

1987 *Siphloplecton* sp. DEMOULIN, 1968. – HUBBARD, p. 46 (list of synonymy).

Material: Female imago, DEMOULIN (1968: 254, fig. 19). STANTIEN & BECKER collection, GZG.

Stratum typicum: Eocene, Baltic amber.

Description. – DEMOULIN (1968) figured this female specimen that was unfortunately almost completely covered with a thin layer of darker amber hiding any details on head, thorax, abdomen, wing bases, and legs. Moreover, left wings and also apical part of right forewing were not

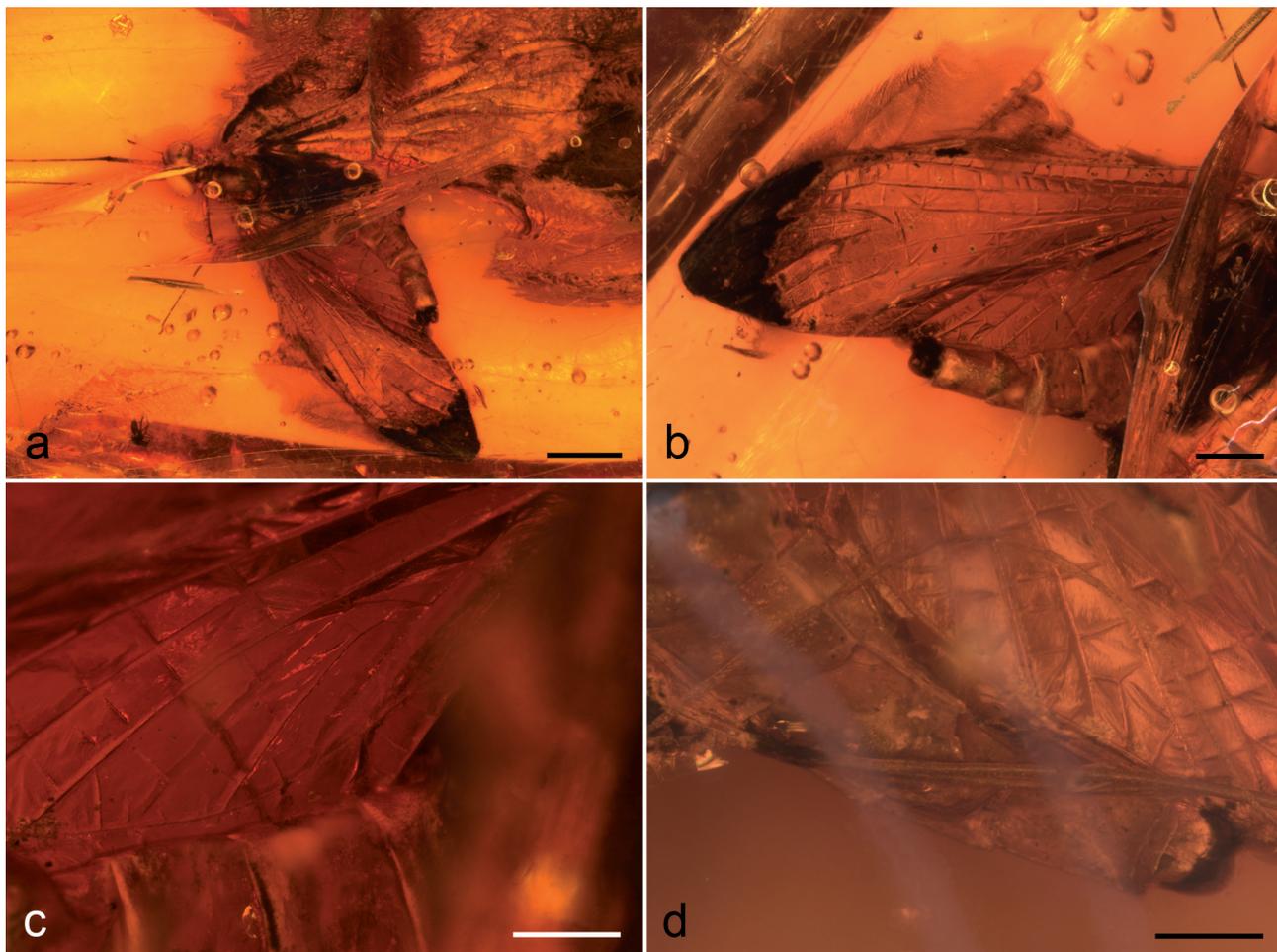


Fig. 15. *Siphloplecton* sp. 4, female imago. – a. General dorsal view. b. Left forewing in dorsal view. c. Cubital field of left forewing in dorsal view. d. Posterior part of abdomen in ventral view. – Scale lines 2 mm (a), 1 mm (b), 0.5 mm (c, d).

preserved. The remaining part of the right forewing clearly showed two pairs of intercalaries in the cubital field. The specimen was embedded in a lateral position, but DEMOULIN neither described the female subgenital and subanal plates nor figured these characters in detail. DEMOULIN already stated that its poor state of conservation made it difficult to draw further conclusion on its specific assignment.

Remarks. – This specimen also belonged to the STANTIEN & BECKER collection, but it could not be anymore located in the GZG where this collection is housed today. As the specimen appears to be lost, there is no reinvestigation possible, so this specimen cannot be assigned to a certain species.

3.1.1.7.4. *Siphloplecton* sp. 4
(fig. 2 in DEMOULIN 1970)
Fig. 15

1970 *Siphloplecton ?macrops* (PICTET, 1856). – DEMOULIN, p. 2, fig. 2 (description).

1987 *Siphloplecton ?macrops*. – HUBBARD, p. 46 (list of synonymy).

Material: Female imago, DEMOULIN (1970: 2, fig. 2), originally labeled: “4690 Ephémères”. BURSEY collection, MNHN.

Stratum typicum: Eocene, Baltic amber.

Description. – Female specimen visible in dorsal and ventral aspect (Fig. 15). It is complete except of right hind leg not preserved and terminal filaments broken. Due to some distortions of amber, pterothorax, hind wings, and anterior part of abdomen hardly visible. DEMOULIN (1970) figured this female specimen and tentatively attributed it to *Siphloplecton* sp. We could not attribute this specimen with certainty to a described species because its subgenital plate is only partly visible (Fig. 15d).

3.1.2. Genus *Metretopus* EATON, 1901

In contrast to other genera of Metretopodidae, the genus *Metretopus* is characterized in the winged stages by

the presence of one pair of intercalaries in the cubital field of forewing.

There are three extant species of *Metretopus* described: *Metretopus borealis* EATON, 1871 has a Holarctic distribution, while *M. alter* BENGTSOON, 1930 and *M. tertius* TIUNOVA, 1999 are confined to the Palearctic region (BERNER 1978, KLUGE 2004). The male genitalia of *Metretopus* have a characteristic, elongate shape without medial incision at half-length unlike in *Siphloplecton* (see BERNER 1978, fig. 11).

So far there are only two fossil species formally described within the genus, namely *Metretopus? henningseni* DEMOULIN, 1965 and *Metretopus trinervis* DEMOULIN, 1968.

3.1.2.1. *Metretopus? henningseni* DEMOULIN, 1965
(fig. 1 in DEMOULIN 1965)
Fig. 16

1965 *Metretopus? henningseni* DEMOULIN, 1965. – DEMOULIN, p. 144 (description, designation of holotype).

1965 *Metretopus? henningseni* [sic!] DEMOULIN, 1965. – DEMOULIN, fig. 1 (description, designation of holotype).

1968 *Metretopus henningseni* DEMOULIN. – DEMOULIN, p. 249 (comparison with *M. trinervis*).

1987 *Metretopus henningseni* DEMOULIN, 1965. – HUBBARD, p. 45 (list of synonymy).

1998 *Metretopus henningseni* DEMOULIN, 1965. – WEITSCHAT & WICHARD, p. 94 (species list).

2004 [*Metretopus*] *henningseni* DEMOULIN, 1965. – KLUGE, p. 356 (in *Anteritorna* inc. sed.).

2009 *Metretopus henningseni* DEMOULIN, 1965. – WICHARD et al., p. 291 (species list).

Holotype: Isolated imaginal right forewing designated as holotype by DEMOULIN (1965: 144, fig. 1), ZMUC (Fig. 16).

Stratum typicum: Eocene, Baltic amber.

Description of holotype. – Isolated right imaginal forewing in mediocre condition, basal part hardly visible (Fig. 16a, b). Pterostigma with numerous anastomosed veins. MA forked at about half length. MP2 basally connected to MP1. iMP basally approximated to MP1,

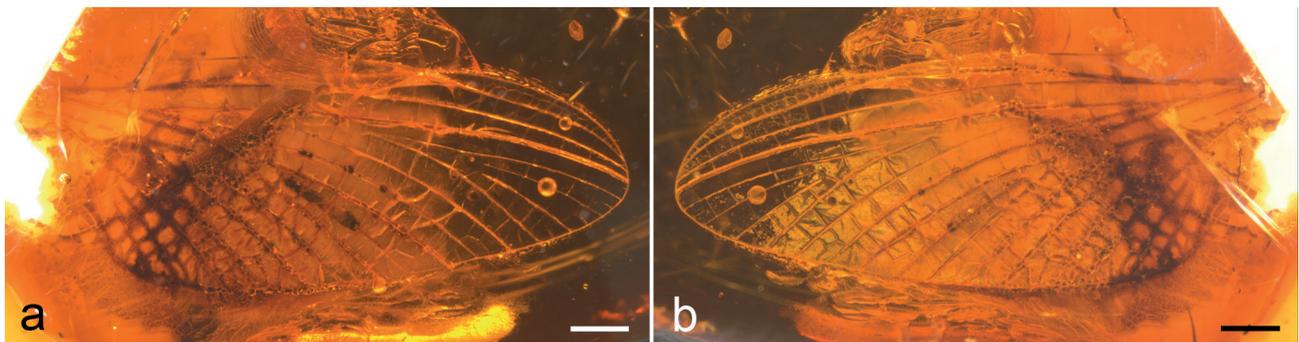


Fig. 16. Ephemeroptera inc. sed. (isolated imaginal right forewing, holotype of *Metretopus? henningseni* DEMOULIN, 1965). – a. Dorsal view. b. Ventral view. – Scale lines 1 mm.

almost reaching MP fork. Cubital field with two long intercalaries. Anterior intercalary vein basally connected to CuA by cross vein, posterior intercalary vein only little shorter, basally connected to anterior intercalary vein by short cross vein. Basal part of CuP and AA not preserved.

Discussion. – DEMOULIN (1965) described an isolated right forewing as *Metretopus? henningseni*, at the same time he admitted that his assignment of this wing to the genus *Metretopus* was provisional. Later, DEMOULIN (1968) even suggested that this specimen might also be placed within Heptageniidae. KLUGE (2004) assigned this specimen to *Anteritorna* inc. sed. without comment.

Contrary to our own observation, in DEMOULIN's (1965) wing drawing a long iMP is connected with MP1, and a shorter MP2 is apically connected with iMP rather than connected with MP1. A reason for the differences in observation may be due to our treatment of the brittle amber that was partly polished and embedded in resin. As a result of this treatment, medial and cubital fields are now much better visible with less distortions, so we are able to confirm that MP2 is indeed basally connected with MP1, and iMP basally approximated to MP1, almost reaching fork MP fork.

However, the combination of these wing characters is not only present in *Metretopus*, but for instance also in some fossil and Recent Ameletidae, namely *Electroletus soldani* GODUNKO & NEUMANN, 2006 and *Metreletus balcanicus* (ULMER, 1920) (see GODUNKO & NEUMANN 2006). So we agree with KLUGE (2004) that this specimen cannot be placed within *Metretopus* with certainty, and as a consequence we transfer *Metretopus? henningseni* DEMOULIN, 1965 to Ephemeroptera inc. sed.

3.1.2.2. *Metretopus trinervis* DEMOULIN, 1968 (figs. 12, 13 in DEMOULIN 1968) Figs. 17–20

- 1968 *Metretopus trinervis* DEMOULIN, 1968. – DEMOULIN, p. 247, figs. 12, 13a, b (description, designation of holotype, allotype and paratype).
1987 *Metretopus trinervis* [sic!] DEMOULIN, 1968. – HUBBARD, p. 45 (list of synonymy).
1998 *Metretopus trinervis* DEMOULIN, 1968. – WEITSCHAT & WICHARD, p. 94 (species list).
2004 [*Metretopus*] *trinervis* DEMOULIN, 1968. – KLUGE, p. 356 (in *Anteritorna* inc. sed.).
2009 *Metretopus trinervis* DEMOULIN, 1968. – WICHARD et al., p. 291 (species list).

Holotype: Male subimago designated as holotype by DEMOULIN (1968: 248, fig. 12), STANTIEN & BECKER collection, GZG (Figs. 17, 18).

Allotype: Female subimago designated as paratype of *Metretopus trinervis* by DEMOULIN (1968: 148, fig. 13a), originally labeled 3B867, STANTIEN & BECKER collection, GZG (Fig. 19).

Paratype: Female subimago designated as paratype of *Metretopus trinervis* by DEMOULIN (1968: 148, fig. 13b), originally labeled 3B871, STANTIEN & BECKER collection, GZG (Fig. 20).

Stratum typicum: Eocene, Baltic amber.

Description of holotype. – Male subimago embedded on slide, visible in dorsal and ventral view (Fig. 17a, b). Specimen rather poorly preserved with apical parts of forelegs and cerci lost, and right hind wing twisted. Dorsal (Fig. 18a) and ventral (Fig. 18b) side of head, thorax, and apical part of abdomen with considerable amount of “Verlumung”. Abdominal tip, posterior parts of hind wings and left forewing darkened. Genitalia not visible.

Eyes contiguous medially. Pigmentation of mesothorax not visible. Mesonotal suture and anterior parts of

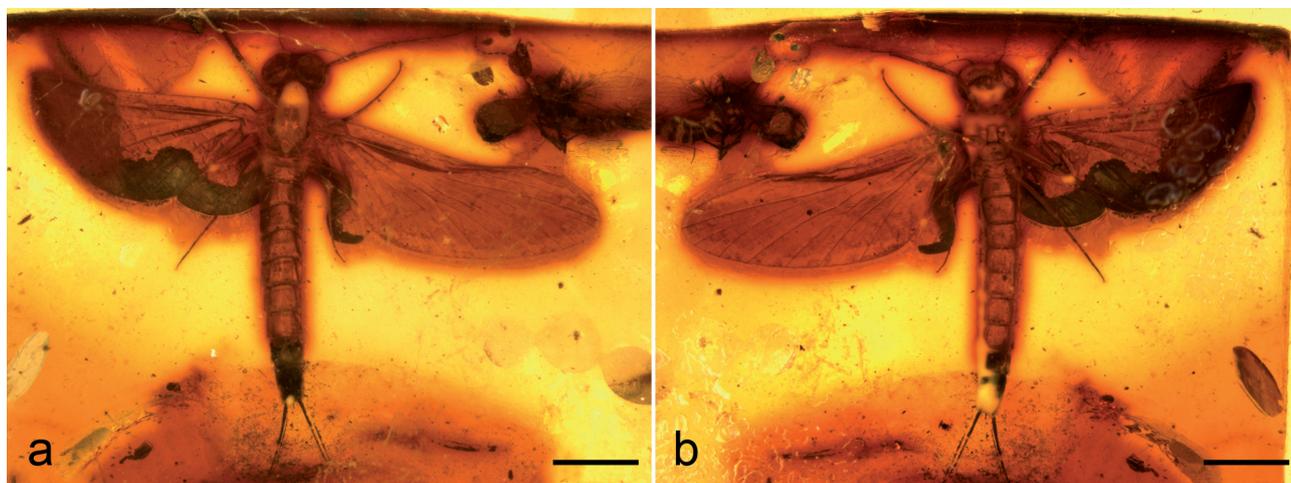


Fig. 17. *Metretopus trinervis* DEMOULIN, 1968; holotype, male subimago. – a. General dorsal view. b. General ventral view. – Scale lines 2 mm.

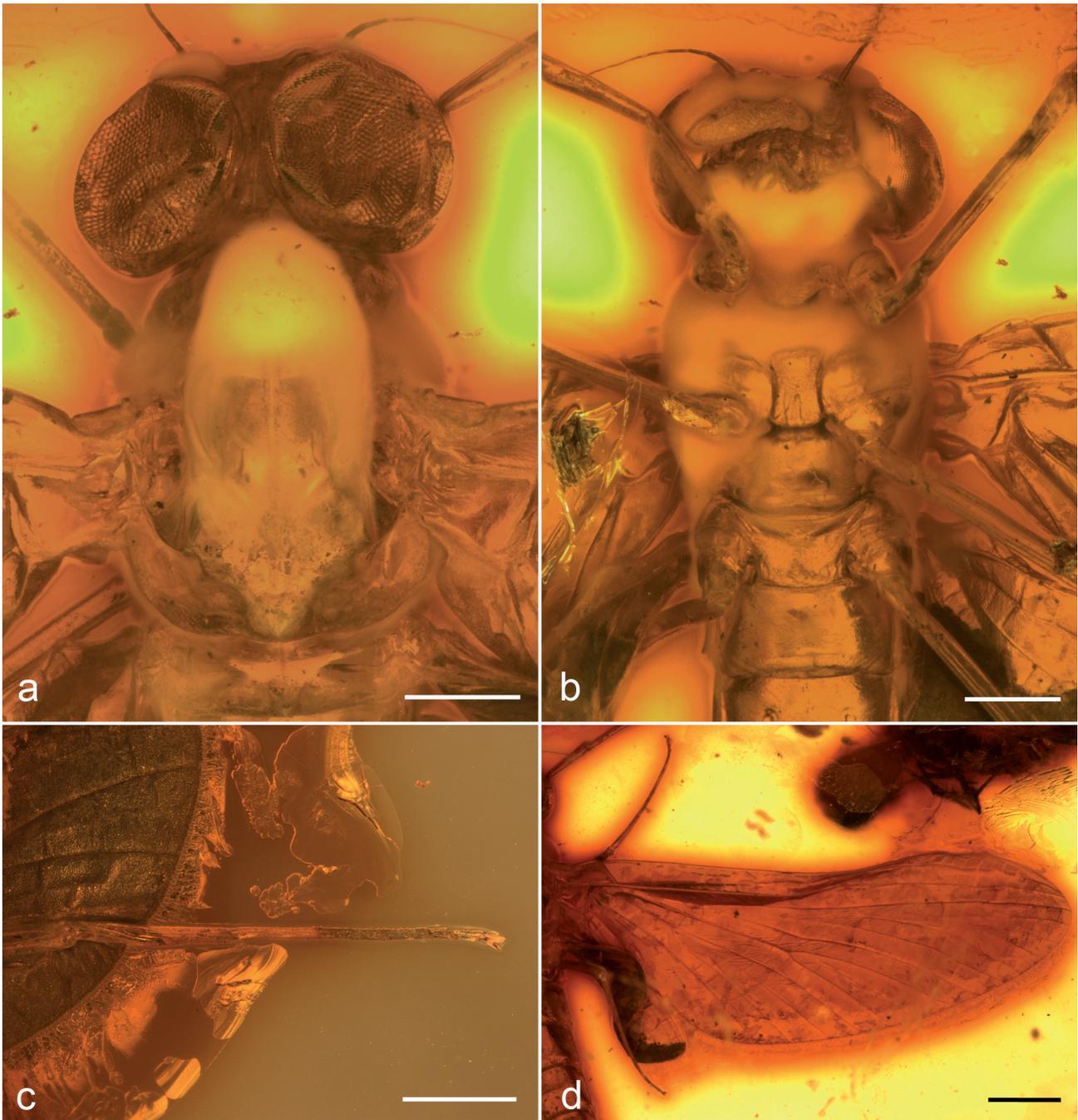


Fig. 18. *Metretopus trinervis* DEMOULIN, 1968; holotype, male subimago. – **a.** Head and thorax in dorsal view. **b.** Thorax in ventral view. **c.** Left hind leg in ventral view. **d.** Cubital field of right forewing in dorsal view. – Scale lines 0.5 mm (a, b, c), 1 mm (d).

mesoparapsidal and lateroparapsidal sutures covered by “Verlummung”, only posterior parts preserved. Mesosternum with contiguous furcasternal protuberances. Wings opaque with setation on posterior margins. Pterostigma with several cross veins, not anastomosed. Cubital field of forewings each with two intercalaries, anterior intercalary vein smaller, basally connected with CuA, posterior inter-

calary longer, connected to CuA with several cross veins (Fig. 18d). Hind wing with acute costal process.

First tarsal segment of mid and hind legs longest, fused with tibia (Fig. 18c). Tibiopatellar suture well visible in mid and hind leg. Middle and hind legs 5-segmented. Tarsal claws dissimilar (one claw hooked, other one blunt). Paracercus vestigial.

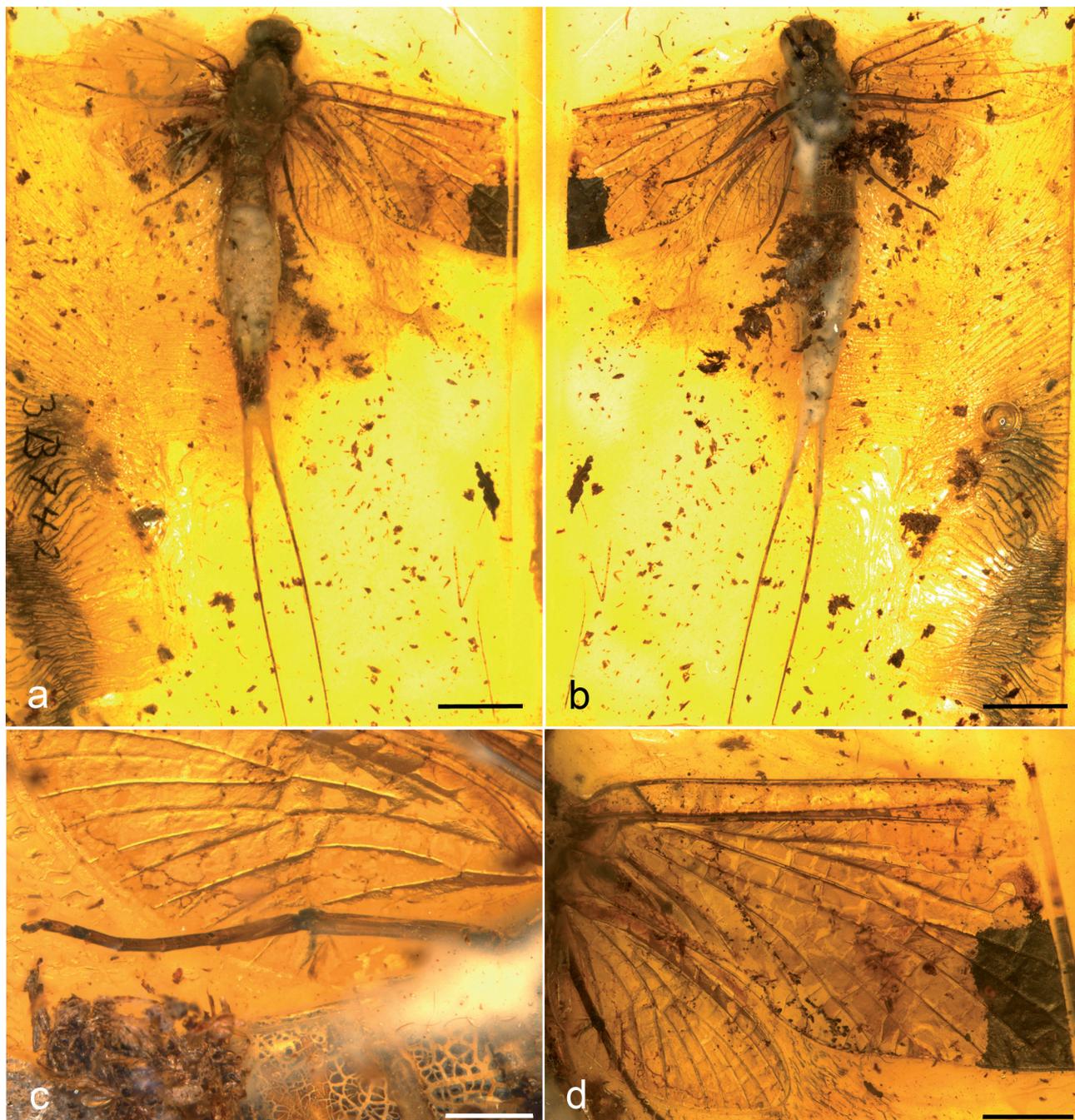


Fig. 19. *Metretopus* sp. (allotype of *M. trinervis* in DEMOULIN 1968), female subimago. – **a.** General dorsal view. **b.** General ventral view. **c.** Right hind leg in ventral view. **d.** Right fore and hind wing in dorsal view. – Scale lines 2 mm (a, b), 0.5 mm (c), 1 mm (d).

Discussion. – KLUGE (2004) placed *M. trinervis* within *Aneritorna* inc. sed. without any comments, but we can confirm DEMOULIN's placement of holotype and allotype to the genus *Metretopus* by the combination of its diagnostic characters (contiguous furcasternal protuberances, tarsus 5-segmented, tarsomere 1 longest, fused to tibia, cubital field of forewing with one pair of intercalar-

ies, paracercus vestigial). However, a comparison with extant species of *Metretopus* is not possible, because the genital structures are almost entirely covered by "Verlummung" except of the outermost margin of forceps.

Description of allotype. – Female subimago embedded on slide, visible in dorsal and ventral view (Fig. 19a, b). For measurements see Tab. 6. Specimen rather

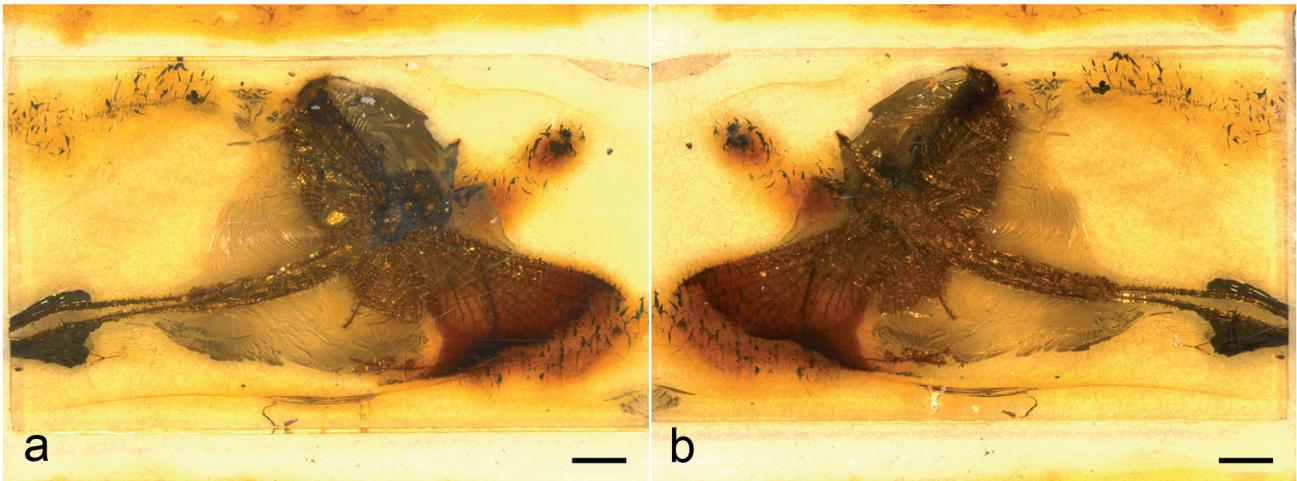


Fig. 20. Ephemeroptera inc. sed. (paratype of *M. trinervis* in DEMOULIN 1968), female subimago. – **a.** General dorsal view. **b.** General ventral view. – Scale lines 2 mm.

poorly preserved with apical parts of both forewings lost, both forelegs lost. Pigmentation of mesothorax not visible. Mesonotal suture nearly transverse, lateral sides of thorax hardly visible; mesoparapsidal and lateroparapsidal sutures covered by “Verlumung”. Mesosternum also hardly visible

because of “Verlumung”, but apparently with contiguous furcasternal protuberances. Wings with setation on posterior margins. Apical half of abdomen dorsally (Fig. 19a) and ventrally (Fig. 19b) with considerable amount of “Verlumung”. Genitalia not visible.

Tab. 6. Measurements of *Metretopus* sp. (female subimago, allotype of *M. trinervis* in DEMOULIN 1968). * = preserved part.

Characters	(mm)
Length of body	10.00
Length of right foreleg	–
Length of femur	–
Length of tibia	–
Length of tarsus	–
Segment 1	–
Segment 2	–
Segment 3	–
Segment 4	–
Segment 5	–
Length of left foreleg	–
Length of femur	–
Length of tibia	–
Length of tarsus	–
Segment 1	–
Segment 2	–
Segment 3	–
Segment 4	–
Segment 5	–
Length of right middle leg	3.24
Length of femur	1.28
Length of tibia	0.81
Length of tarsus	1.15
Segment 1	0.38
Segment 2	0.26
Segment 3	0.24
Segment 4	0.14
Segment 5	0.13
Length of left middle leg	3.48
Length of femur	1.28
Length of tibia	0.83

Length of tarsus	1.37
Segment 1	0.41
Segment 2	0.37
Segment 3	0.36
Segment 4	0.10
Segment 5	0.13
Length of right hind leg	2.54
Length of femur	1.09
Length of tibia	0.52
Length of tarsus	0.93
Segment 1	0.26
Segment 2	0.25
Segment 3	0.19
Segment 4	0.07
Segment 5	0.16
Length of left hind leg	1.79*
Length of femur	–
Length of tibia	0.62
Length of tarsus	1.17
Segment 1	0.40
Segment 2	0.32
Segment 3	0.23
Segment 4	0.08
Segment 5	0.14
Length of right forewing	4.71*
Length of left forewing	4.71*
Length of right hind wing	3.24
Length of left hind wing	3.24
Hind/forewings length ratio	–
Length of right cercus	7.35
Length of left cercus	7.35

Pterostigmata not preserved. Cubital field of forewings each with two intercalaries, anterior intercalary vein longer, basally connected with CuA by cross veins, posterior intercalary shorter, connected only with anterior intercalary (Fig. 19d). Hind wing with costal process (Fig. 19b).

First tarsal segment of mid and hind legs longest, fused with tibia (Fig. 19c). Tibiopatellar suture well visible in mid and hind leg. Middle and hind legs 5-segmented. Tarsal claws dissimilar (one claw hooked, other one blunt). Paracercus not visible because of “Verlummung”, but obviously vestigial.

D i s c u s s i o n . – While the combination of diagnostic characters (contiguous furcasternal protuberances, tarsus 5-segmented, tarsomere 1 longest, fused to tibia, cubital field of forewing with one pair of intercalaries, paracercus vestigial) makes it likely that this specimen can be attributed to *Metretopus*, there is no character available that could link this female subimago to *Metretopus trinervis*. Additionally, a comparison with extant species of *Metretopus* is not possible, because the genital structures are not visible. As a consequence, we refrain from a formal assignment to a new species and treat this specimen as *Metretopus* sp.

D e s c r i p t i o n o f p a r a t y p e . – Female subimago embedded on slide, visible in dorsal and ventral aspect (Fig. 20a, b). Specimen in very poor condition, amber very brittle with multiple cracks all over the specimen, additionally right forewing darkened due to oxidation. Apical part of left forewing, tarsus of left foreleg, both hind legs, and apical part of cerci lost. Pigmentation of mesothorax not visible. Thoracic sutures not clearly visible due to amber distortions. Mesosternum also hardly visible, but apparently with contiguous furcasternal protuberances. Wings with setation on posterior margins. Details of leg segmentation, abdomen and genitalia not discernible.

Pterostigmatic region of right forewing without reticulation. Cubital field of right forewing hardly discernible, apparently with two intercalaries, anterior intercalary vein longer, basally connected with CuA by cross veins, posterior intercalary shorter, connected only with anterior intercalary (Fig. 19d). Hind wing with costal process (Fig. 19b).

D i s c u s s i o n . – The poor preservation does not allow a firm assignment to a mayfly family, so we treat this specimen as Ephemeroptera inc. sed.

4. Conclusions

The reinvestigation of all available type material of fossil Metretopodidae revealed surprising new insights in the fossil history of this taxon. The assignment of the previously described *Metretopus? henningseni* to *Metretopus* could not be confirmed, so the two subimagines assigned to *M. trinervis* and *Metretopus* sp. remain the only certain

fossil records of this genus at present. Much greater species diversity in the hitherto described specimens of *Siphloplecton* could be observed than previously recognised. We are aware of the fact that we may have discovered males and females that represent the same species, but at present there are no characters available which would allow attributing different male and female morphotypes to a certain common species. As a consequence, all male and female specimens that clearly differed from each other in their respective genitalia or subanal plates were each attributed to different species. The addition of four new species leads to a total of six formally described fossil species of *Siphloplecton*: *S. macrops* PICTET-BARABAN & HAGEN, 1856; *S. picteti* sp. nov.; *S. barabani* sp. nov.; *S. hageni* sp. nov.; *S. jaegeri* DEMOULIN, 1968; and *S. demoulini* sp. nov.

We are also aware of the fact that one of the newly described species may be conspecific with the previously described *S. macrops*. However, as its holotype is lost and as there is no detailed description or figure of its genitalia available, a conspecificity cannot be proven.

The present study was intended as a first step to enable studies on new material of fossil Metretopodidae. In future contributions we will thus add new specimens to the species described herein and also describe further new species of fossil Metretopodidae from different collections.

5. References

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Addresses of the authors:

Dr. ARNOLD H. STANICZEK, Staatliches Museum für Naturkunde Stuttgart, Abteilung Entomologie, Rosenstein 1, 70191 Stuttgart, Germany
E-mail: arnold.staniczek@smns-bw.de

Dr. ROMAN J. GODUNKO, State Museum of Natural History, National Academy of Sciences of Ukraine, Teatralna 18, 79008 Lviv, Ukraine; and Biology Centre of the Academy of Sciences of the Czech Republic, Institute of Entomology, Branišovská 31, 37005 České Budějovice, Czech Republic
E-mail: godunko@seznam.cz
godunko@museum.lviv.net