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# The Imitation Game: In Search for Brachycera in the Triassic

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**Abstract:** The richest assemblage of the Triassic Diptera has been described from the famous Konservat-Lagerstätte Grès à Voltzia (Upper Buntsandstein) in the northern Vosges Mountains in France, dated as Early Anisian. A re-examination of the holotypes and additional material from the type locality allows for the establishment of *Vogerhyphus* gen. nov. and erection of the Vogerhyphinae subfam. nov. for *Vymrhyphus blagoderovi* Krzemiński and Krzemińska, 2003 and *Vogerhyphus krzeminskorum* sp. nov. (Protorhyphidae), and a new monotypic family Galliidae fam. nov. for *Gallia alsatica* Krzemiński and Krzemińska, 2003, originally described as Rhagionidae based on its wing venation. Galliidae fam. nov. is characterized by its closed *cua* cell and long moniliform antenna with 14-segmented flagellum and is hypothesized to belong to the stem-group Brachycera, along with the Late Triassic Prosechamyiidae. The process of brachycerization in the Diptera evolution is briefly discussed.

**Keywords:** Anisian; Grès à Voltzia; Upper Buntsandstein; fossil insects; new taxa; true flies

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## 1. Introduction

The oldest fossil Diptera come from the Anisian deposits in Spain, Germany and France [1–3]. The richest Triassic assemblage of Diptera has been described from the famous Konservat-Lagerstätte Grès à Voltzia (Upper Buntsandstein) of the northern Vosges Mountains in France (hereinafter referred to as the Vosges), dated as Bithynian, about 245 Ma. For outcrops of the Vosges, a deltaic area is reconstructed, a transitional environment ranging from nearshore to terrestrial, with unstable and occasionally hash conditions, and numerous shallow drying pools [4,5]. The assemblage from the Vosges comprises about 70 adults, 30 pupae and 3 larvae [6] representing Nematocera of the infraorders Tipulomorpha, Psychodomorpha *sensu* Hennig, Culicomorpha and Bibionomorpha, as well as Brachycera. The very first dipteran described from these beds was *Grauvogelia arzvilleriana* Krzemiński, Krzemińska and Papier 1994, based on numerous well-preserved isolated wings [1]. Krzemiński and Krzemińska [7] added another five species (four of them in new genera), each based on a single adult specimen: *Louisa nova* Krzemiński and Krzemińska, 2003 (Grauvogeliidae), *Tanus triassicus* Krzemiński and Krzemińska, 2003 (Nadipteridae), *Archilimonia vogesiana* Krzemiński and Krzemińska, 2003 (Archilimoniidae), *Vymrhyphus blagoderovi* Krzemiński and Krzemińska, 2003 (Protorhyphidae), and *Gallia alsatica* Krzemiński and Krzemińska, 2003 (Rhagionidae). The type of *A. vogesiana* was revised as a member of the Limoniidae and a second species, *A. grauvogeliana* Lukashevich and Ribeiro, 2019, was described from the Vosges [8]. Recently, the holotype of *T. triassicus* was re-examined, some details of the wing venation were clarified, and photographs were published for the first time [2].

The present paper deals with some undescribed adult Diptera from the Vosges, also collected by Louis Grauvogel in the middle of the 20th century [9]. The holotypes of

*Vymrhyphus blagoderovi* and *Gallia alsatica* were re-examined by EDL in 2008, and their photographs are published herein for the first time.

It was already suggested that *Vymrhyphus blagoderovi* from the Vosges belongs in a separate genus, although no new name was proposed at the time [10]. In a key to the genera of the Protorhyphidae [11], this species was also separated from its congeners. A re-examination of the holotype and additional material from the type locality allows us to establish a new genus in a new subfamily for this peculiar taxon.

For twenty years after the description of *Gallia alsatica*, no additional Rhagionidae and only one other brachyceran genus was described as a member of the monotypic Pro-sechamyiidae [10] from Triassic deposits. Thus, Brachycera have been (expectedly) extremely rare in the Triassic fossil record, with only the three described specimens. Additional *Gallia* specimens from the Vosges and re-examination of the holotype of *G. alsatica* prompts the erection of a new family for this unusual genus based on characteristics other than wing venation.

## 2. Material and Methods

Several thousands of insects are known from 13 localities in the northern Vosges from the lowermost unit of ‘Grès à Voltzia’ Formation, which is part of the Upper Buntsandstein, dating to the early Anisian [12]. All the specimens discussed below were found in Arzviller (Moselle department), as well as some other 80 dipterans from the Vosges, from the same lens 118b, intercalated within fluviatile sandstones [13]. The material had been housed in the private collection of Léa Grauvogel-Stamm, Strasbourg, France, for many years, until 2017, when these fossils were transferred to the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS). In our paper, SMNS accession numbers are used. In earlier publications dealing with this material [2,7,8], accession numbers from different collections (where material was housed previously) were published—herein, they are given in brackets, e.g., SMNS-P-75643-1 (No. 9077). Parts and counterparts are specified with a slash, e.g., SMNS-P-7543-2/3, unless otherwise stated.

The specimens were photographed using a Leica MZ9.5 stereomicroscope with a Leica DFC420 digital camera, and the images were edited using Adobe Photoshop CS 9.0 software. The orientation of the published photographs reflects the actual position of the specimens, whereas line drawings are flipped for ease of comparison.

The wing vein terminology used in this study follows that of Shcherbakov et al. [14] and Mostovski et al. [15]. The anal cell *auct.* is accepted here as *cua*.

## 3. Results

Infraorder Bibionomorpha.
Family Protorhyphidae Handlirsch, 1906.
Subfamily Protorhyphinae Handlirsch, 1906.

Type genus: *Protorhyphus* Handlirsch, 1906 (Dobbertin, Germany, $J_1$).

Diagnosis: Sc moderate or short with apex near or before wing midlength; crossvein *r-m* connecting $R_{4+5}$ and $M_{1+2}$ stems; basal part of M thin, desclerotized; discal cell near wing midlength; $M_{1+2}$ fork longer than $M_{3+4}$ fork; Rs origin at 0.17–0.33, M forking at 0.33–0.44, CuA apex at 0.44–0.56 wing length; $A_1$ short.

Composition: In addition to the type genus, *Archirhyphus* Handlirsch, 1939, *Vymrhyphus* Blagoderov, 1995, *Brachyrhyphus* Blagoderov and Grimaldi, 2007, and *Austrorhyphus* Martin, 2008 from the Mesozoic of Eurasia, North America and Australia.

Subfamily Vogerhyphinae subfam. nov.
LSID: urn:lsid:zoobank.org:act:79A864ED-5560-46B6-9EB8-B65214B53568.
Type genus: *Vogerhyphus* gen. nov. (Vosges, France, $Tr_2$).

Diagnosis: Sc long, with apex beyond wing midlength; crossvein *r-m* connecting $M_{1+2}$ stem with $R_5$ base; basal part of M obvious; discal cell beyond wing midlength; $M_{3+4}$ fork longer than $M_{1+2}$ fork; Rs origin at 0.4, M forking at 0.5, CuA apex at 0.65 of wing length; $A_1$ relatively long and wavy, not reaching wing margin.

Comparison: The new subfamily differs from Protorhyphinae in having a longer Sc, the position of *r-m* connecting $M_{1+2}$ stem with the $R_5$ base, the position of the discal cell in the distal half of the wing, and a relatively shorter $M_{1+2}$ fork.

Composition: The type genus.

*Vogerhyphus* gen. nov.

*Vymrhyphus* Blagoderov, 1995 (partim).

LSID: urn:lsid:zoobank.org:act:B3C86E29-69DF-40EE-A7F9-55C463118ADC.

Type species: *Vymrhyphus blagoderovi* Krzemiński and Krzemińska, 2003 (Vosges, France, $Tr_2$).

Etymology: From Vosges Mountains.

Diagnosis: Wing elongated, 3× longer than wide. Sc long, extending beyond wing midlength, with its apex near or beyond *r-m* level. C ending slightly beyond $R_5$ apex; all radial veins nearly straight and subparallell for most of their length. $R_1$ straight and long (0.75–0.85 of total wing length). $R_{4+5}$ forking level to discal cell midlength. $R_{4+5}$ stem short, Rs stem 2–2.5× as long as $R_{4+5}$ stem, $R_4$ 5–8× as long as $R_{4+5}$ stem. $R_5$ not arched forwards, ending at wing apex, $R_{4+5}$ fork 1.7–1.8× as long as $M_{1+2}$ fork, *r-m* connecting $R_5$ near base and discal cell midlength. Basal part of M sclerotized, aligned with $M_{1+2}$; $M_{3+4}$ forking near $^1/_3$ discal cell length, bas $M_4$ (before *m-cu*) extremely short. CuA subparallel to CuP or converging but not meeting. Anal lobe developed.

Remarks: *Vogerhyphus* gen. nov. has a long $R_1$ (0.75–0.85 of total wing length). In most previously known protorhyphid genera, $R_1$ is shorter (0.55–0.65 of total wing length), with the exception of *Vymrhyphus* (0.67–0.76, EDL unpubl. data) and *Austrorhyphus* (0.8) [11].

Species included: In addition to the type species, *Vogerhyphus krzeminskorum* sp. nov. (Vosges, France, $Tr_2$).

*Vogerhyphus blagoderovi* (Krzemiński and Krzemińska, 2003) comb. nov.

(Figures 1a and 2a)

*Vymrhyphus blagoderovi* Krzemiński and Krzemińska, 2003 [7] (p. 173, Figure 11).

Holotype: SMNS-P-75643-1± (No. 9077±), part and counterpart of isolated wing; Arzviller (lens 118b), Grès à Voltzia (Upper Buntsandstein; Bithynian, Anisian), Vosges Mountains, France.

Description: Wing length 4.2 mm. Sc 0.65 of total wing length; $R_1$ about 0.85 of total wing length, with apex level with $M_2$ apex; Rs stem almost straight, twice as long as $R_{4+5}$ stem; $R_4$ 5× as long as $R_{4+5}$ stem; discal cell 0.2 of total wing length; CuA with bend at *m-cu*, CuA and CuP converging but not meeting.

Remarks: The wing between CuA and CuP apices is crumpled, so the degree of vein proximity can be exaggerated.

*Vogerhyphus krzeminskorum* sp. nov.

(Figures 1b,c and 2b).

LSID: urn:lsid:zoobank.org:act:2ADDE176-6FA9-41FB-ABCB-88AC50EB61CD.

Etymology: After Ewa and Wieslaw Krzemińskis, authors of numerous taxa from the Vosges.

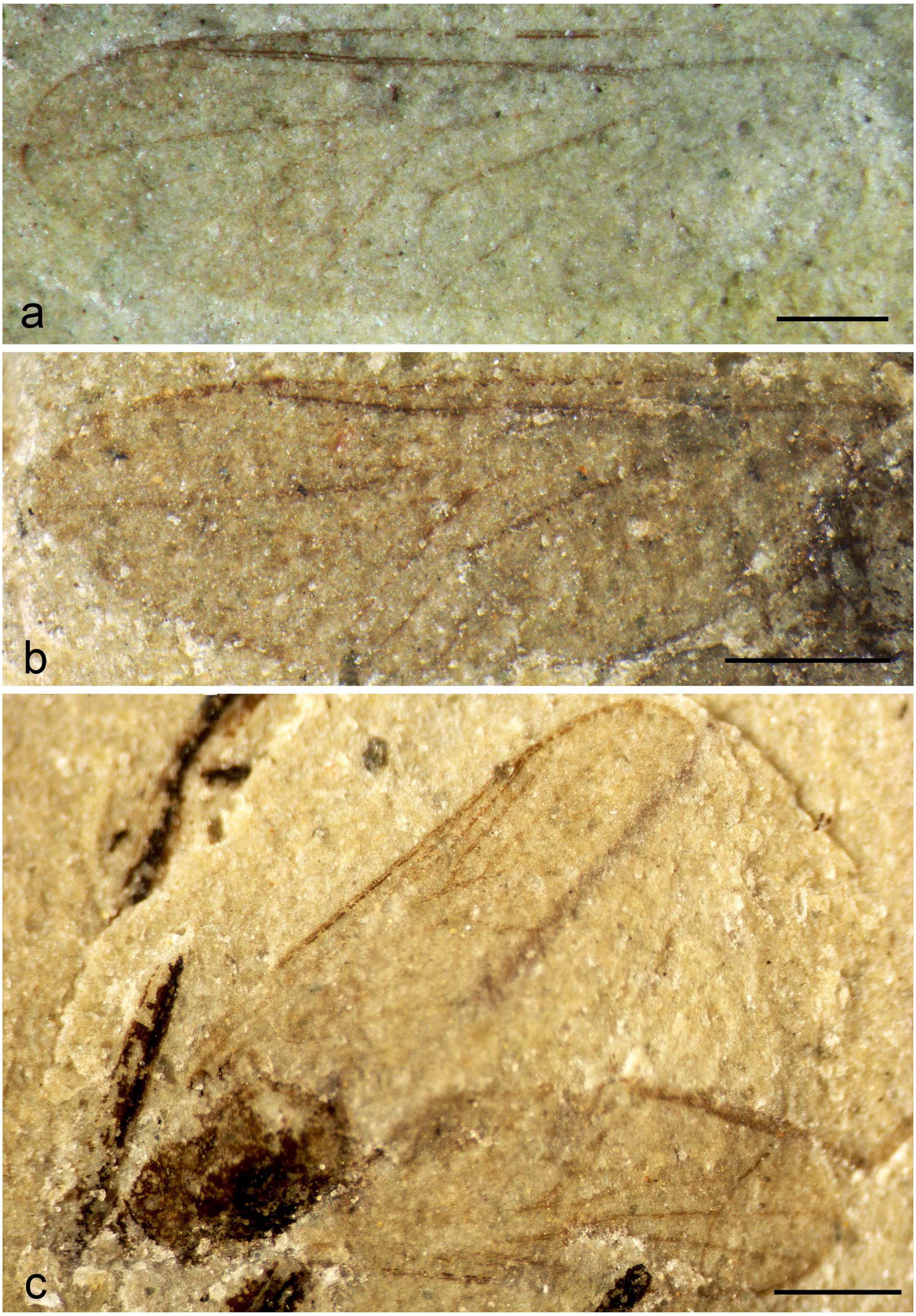

**Figure 1.** *Vogerhyphus*, gen. nov., photograps. (**a**) *V. blagoderovi* (Krzemiński and Krzemińska, 2003) comb. nov., holotype; (**b**,**c**) *V. krzeminskorum* sp. nov., holotype: wing, part; total habitus, counterpart. Scale bars 0.5 mm.

Holotype: SMNS-P-75643-2/3 (No. 5914/5915), part and counterpart of incomplete imago (thorax and both wings preserved); Arzviller (lens 118b), Grès à Voltzia (Upper Buntsandstein; Bithynian, Anisian), Vosges Mountains, France.

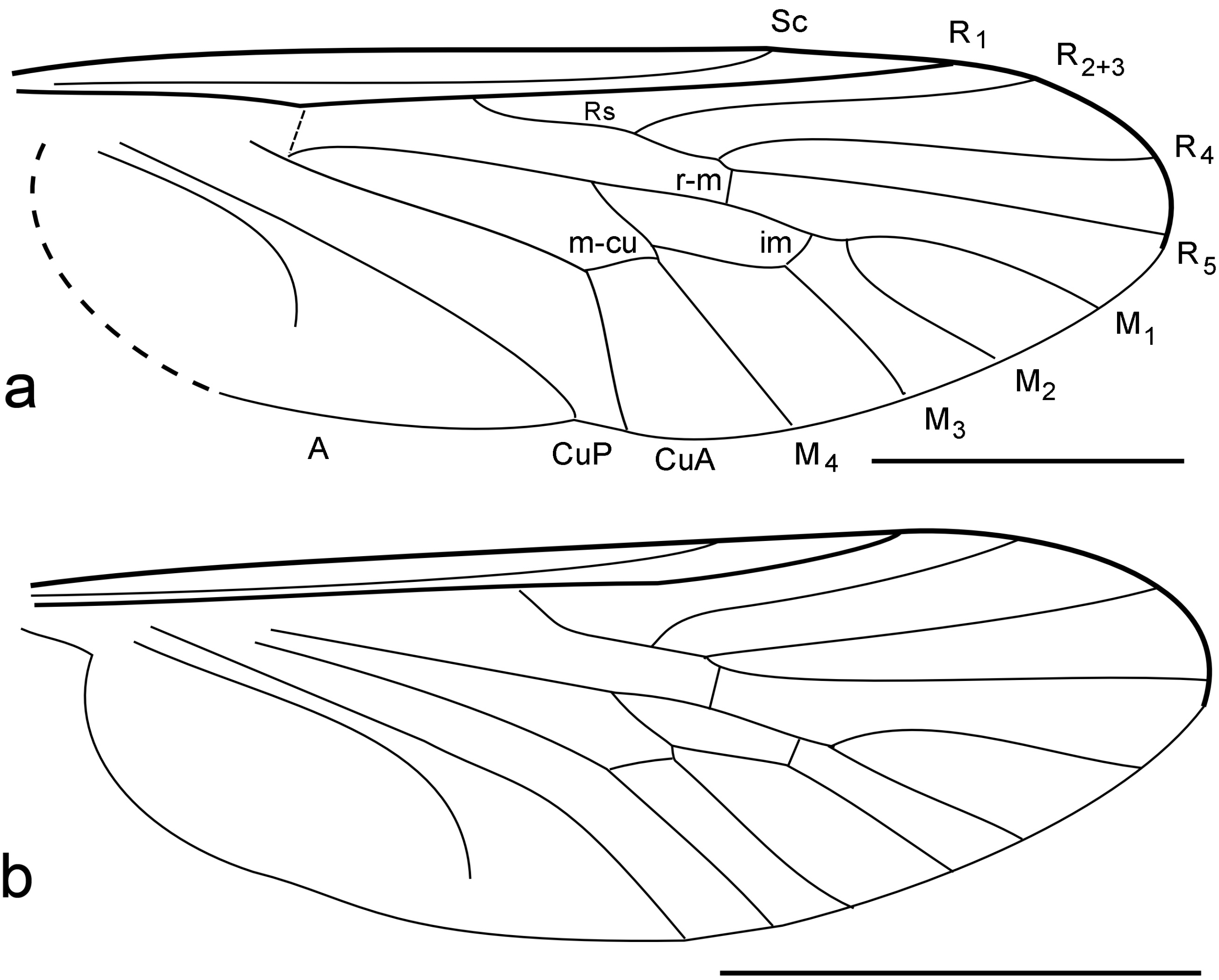

**Figure 2.** Wings of *Vogerhyphus*, gen. nov., line figures. (**a**) *V. blagoderovi* (Krzemiński and Krzemińska, 2003) comb. nov., holotype; (**b**) *V. krzeminskorum* sp. nov., holotype. Scale bars 1 mm.

Description: Wing length 2.7 mm. Sc 0.58 of total wing length; $R_1$ about 0.75 of total wing length, with apex level with $M_3$ apex; Rs stem curved, 2.5× as long as $R_{4+5}$ stem; $R_4$ 8× length of $R_{4+5}$ stem; discal cell 0.17 of total wing length. CuA and CuP subparallel.

Remarks: The new species differs from the type species in the pattern of the cubital veins. The difference in the wing size is considered insignificant. A similar degree of variation has been noted in species of other genera based on numerous isolated wings (*Protorhyphus simplex* Handlirsch, 1906, *P. rohdendorphi* Lukashevich, 2012, and *Archirhyphus asiaticus* Rohdendorf, 1964) [16,17].

The thorax may bear a V-suture, but the state of the material preservation does not allow us to claim this with certainty.

Stem-group Brachycera.
Family Galliidae fam. nov.
LSID: urn:lsid:zoobank.org:act:97047E36-9C8F-47C6-8FA0-99351508F70D.
Type genus: *Gallia* Krzemiński and Krzemińska, 2003 (Vosges, France, $Tr_2$).
Composition: The type genus.

Diagnosis: Antenna long, moniliform, with over 10 more or less uniform segments; short scape and pedicel subequal; first flagellomere likely to be rounded in cross-section, not differing from subsequent flagellomeres; all flagellomeres roughly as long as wide except for 4 apical ones that are slightly elongated. Rs forking beyond M fork, before *r-m* and before or level with Sc apex; $R_1$ and $R_{2+3}$ not converging or diverging at wing margin; $R_{4+5}$ forking noticeably proximad of $R_1$ apex and of distal end of discal cell; $R_{4+5}$ fork much longer than $R_{4+5}$ stem; $R_{4+5}$ fork fairly symmetrical, so Rs, $R_{4+5}$ and $R_5$ do not form a straight line; $R_4$ nearly straight at base and straight apically; $R_5$ ending near wing tip; $M_3$ reaching wing margin; $M_3$ after *im* and $M_4$ (sub)parallel; *m-cu* joining CuA well beyond its midlength; CuA angled at *m-cu*; CuA and CuP meeting at wing margin or cell *cua* with very short petiole.

Comparison: The new family differs from almost all other dipteran families with the closed *cua* cell (anal cell in older terminology) in having a long moniliform antenna with more than eight-segmented flagellum; from the Prosechamyiidae (also with moniliform antenna) in $R_{4+5}$ forking distad of *r-m*, in having all four branches of vein M, closed discal cell and cell *cua* at most with short petiole; and from the Rachiceridae (with more than eight-segmented flagellum) in having non-converging $R_1$ and $R_{2+3}$, $R_{4+5}$ fork proximad of $R_1$ apex and (sub)parallel $M_3$ and $M_4$.

Remarks: The thorax may bear a V-suture, but the state of the material preservation does not allow us to claim this with certainty.

*Gallia* Krzemiński and Krzemińska, 2003.

Diagnosis: Small flies (wing length about 3 mm). Antenna with 16 segments. Sc ending beyond wing midlength; $R_1$ long, ending far beyond $M_{1+2}$ furcation; Rs stem as long as or noticeably longer than $R_{4+5}$; $R_{2+3}$ noticable longer than Rs stem, $R_{4+5}$ fork much longer than its stem; $M_{1+2}$ forking beyond *im*; *m-cu* at or just after $M_{3+4}$ furcation. Abdomen elongate, longer than wing at least in presumptive female, male terminalia not wider than preceding abdominal tergite (Figures 3, 4d,e, 5c and 6a,d).

*Gallia alsatica* Krzemiński and Krzemińska, 2003.

(Figures 3–7).

*Gallia alsatica* Krzemiński and Krzemińska, 2003 [7] (p. 177, Figure 14).

Holotype. SMNS-P-75643-8/9 (No 6170/6171), part and counterpart of male; Arzviller (lens 118b), Grès à Voltzia (Upper Buntsandstein; Bithynian, Anisian), Vosges Mountains, France.

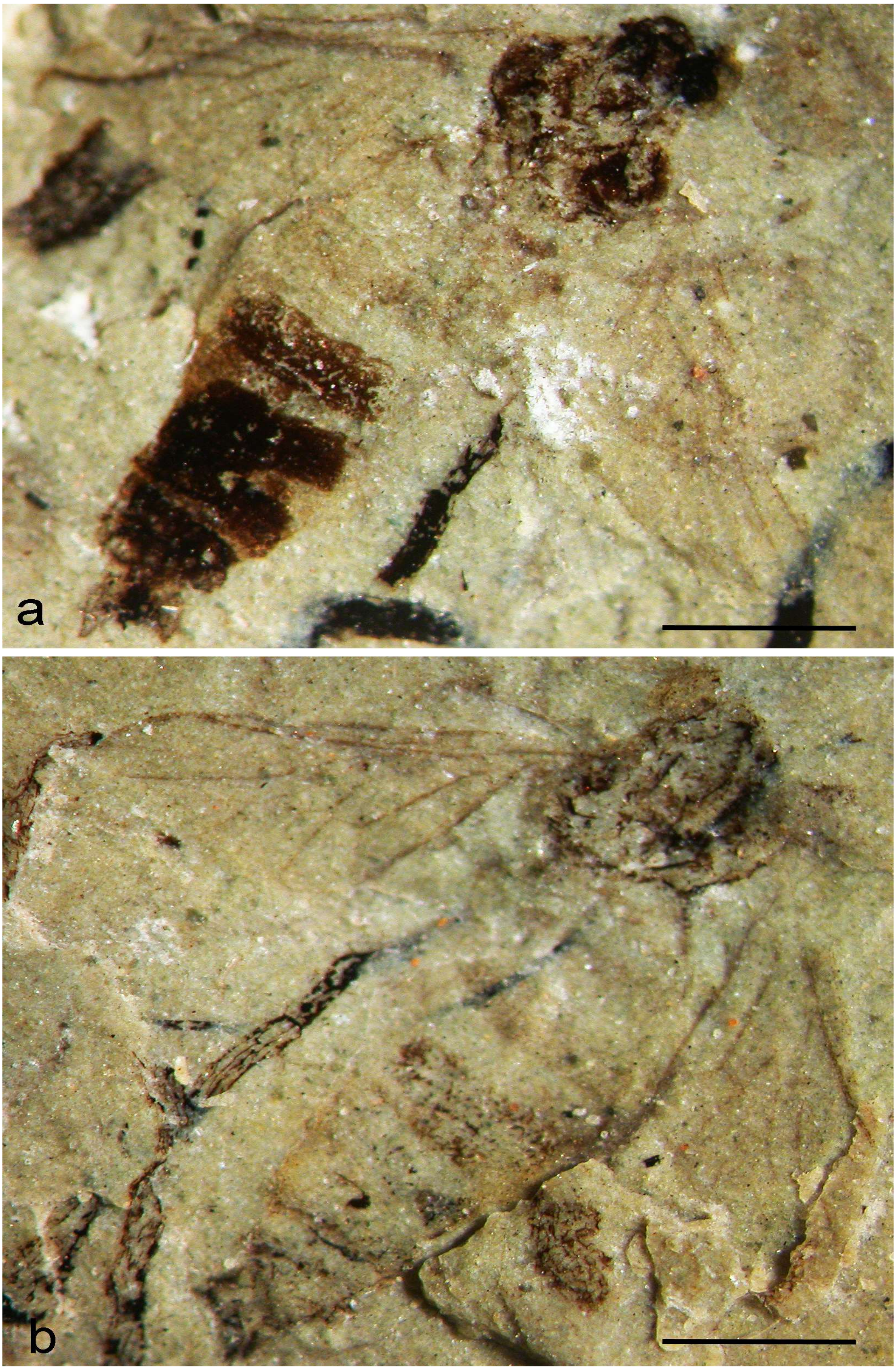

**Figure 3.** *Gallia alsatica* Krzemiński and Krzemińska, 2003, holotype, male, total habitus. (**a**) Part and (**b**) counterpart. Scale bars 1 mm.

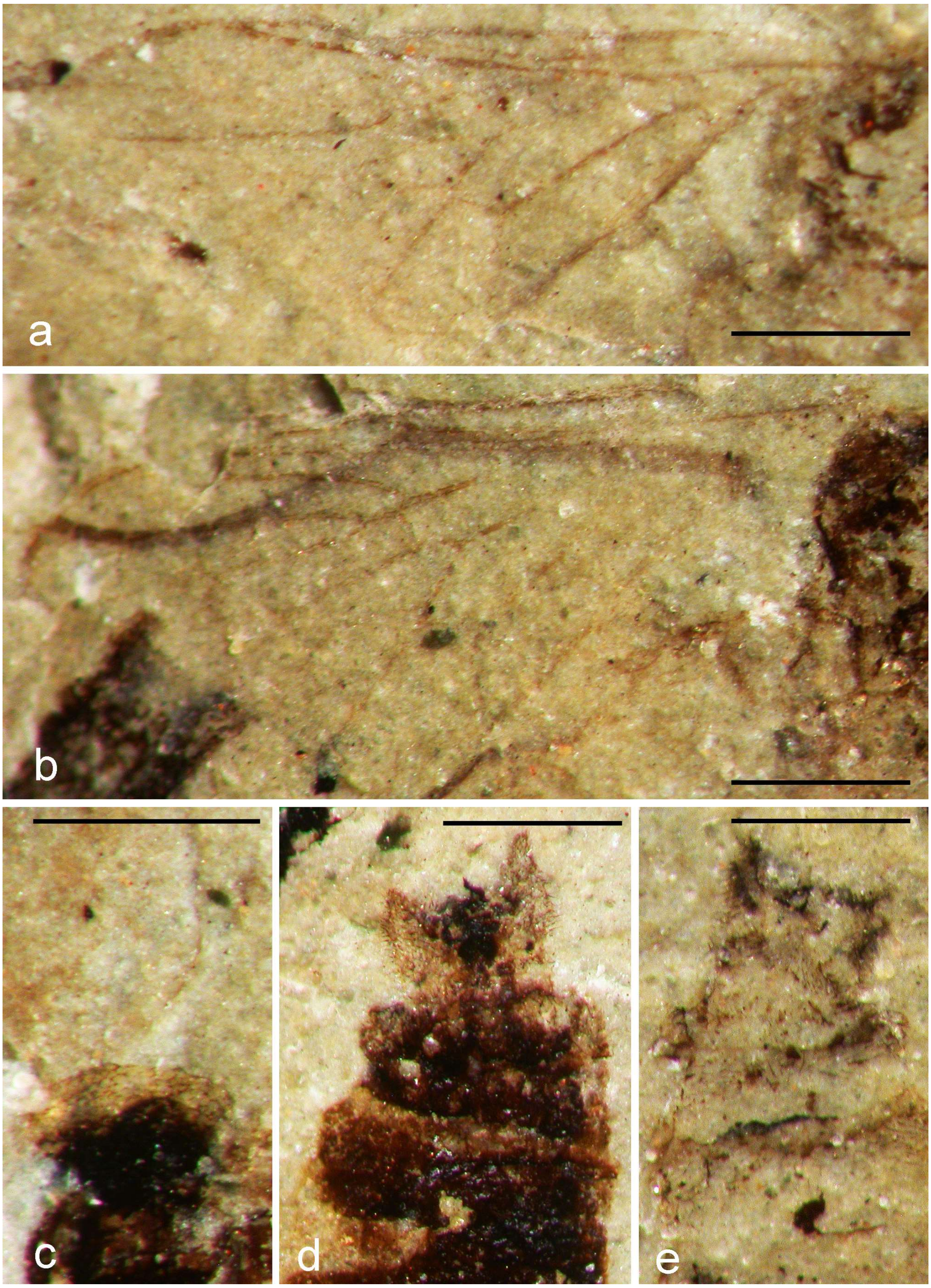

**Figure 4.** Details of *Gallia alsatica* Krzemiński and Krzemińska, 2003, holotype, male, photographs. (**a**) Right wing, counterpart; (**b**) left wing, part; (**c**) head with eye and antenna; (**d**,**e**) abdominal apex, part and counterpart. Scale bars 0.5 mm.

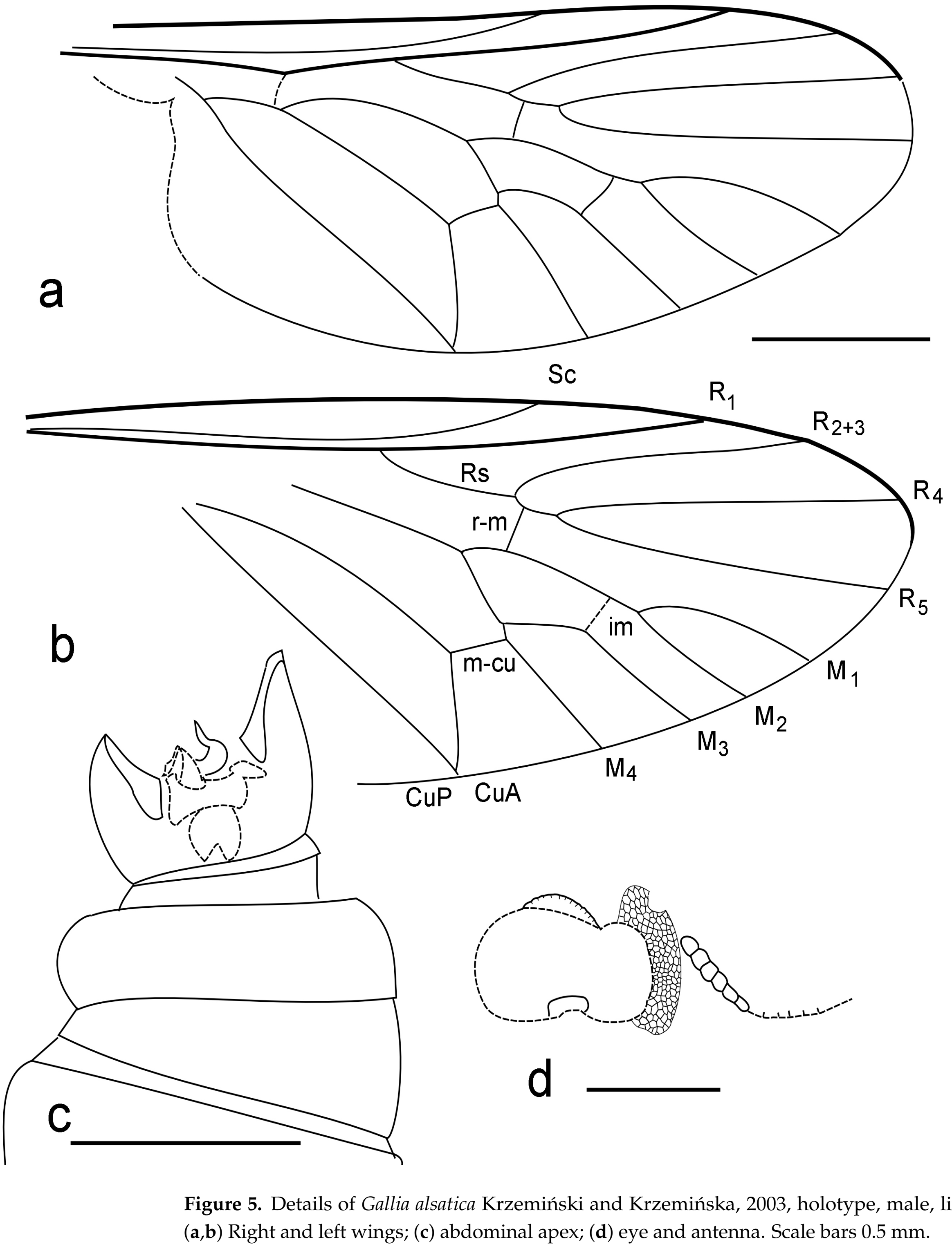

**Figure 5.** Details of *Gallia alsatica* Krzemiński and Krzemińska, 2003, holotype, male, line figures. (**a**,**b**) Right and left wings; (**c**) abdominal apex; (**d**) eye and antenna. Scale bars 0.5 mm.

Additional material: SMNS-P-75643-4/5a (No. 6176a/6177a), possibly female, part and counterpart; SMNS-P-75643-4/5b (No. 6176b/6177b), thorax with two wings, part and counterpart, on one slab with SMNS-P-75643-4/5a; SMNS-P-75643-6/7 (No. 6178/6179), possibly female, part and counterpart; probably from the same slab as SMNS-P-75643-4/5 (the rock is glued on one piece of paper). All additional specimens are from the same lens as holotype.

Description: Head wider than thorax (Figures 6b,d and 7c,d). Eyes large, dichoptic in male, not flattened dorsally, without conspicuous microsetae, facets of male evenly distributed and of equal size (Figures 4c and 5d). Antenna 1.7× longer than head width, with short scape and pedicel of approximately the same size and elongate flagellum, with 14 ovoid flagellomeres, gradually slightly tapered toward apex (Figures 6b–e and 7c,d). Wing moderately long, without distinct colour pattern. Wing venation (Figures 4a,b, 5a,b and 7a,b,c,e): Sc exceeding 0.54–0.57 wing length; arculus present; $R_1$ exceeding 0.75–0.77 wing length; Rs origin at 0.39–0.4 wing length; costal section Sc–$R_1$ clearly longer than $R_1$–$R_{2+3}$; Rs stem 2.2–3.1× as long as $R_{4+5}$ stem in holotype and subequal or 1.5× in other specimens; $R_{2+3}$ nearly straight, ending at C not near $R_{1,}$ 2.0–2.6× in holotype as long as Rs stem and 2.5–3.3× in other specimens; *r-m* dividing $R_{4+5}$ stem as 1:1–2; discal cell 0.17–0.20 of wing length; basal portion of $M_{1+2}$ 4.5–5.2× as long as $M_{1+2}$ after *im* in holotype and 6–10× in other specimens; $M_{3+4}$ fork subequal or 1.2–1.3× as long as $M_{1+2}$ fork; *m-cu* 3–4× as long as basal portion of $M_4$ or basal portion absent. Abdomen about as wide as thorax, anterior five tergites virtually parallel-sided, posterior tergites slightly conically tapered; abdomen and male terminalia pubescent (Figures 3, 4e and 6a,d); aedeagal sheath probably with two stout curved apical hooks (Figures 4d and 5c).

Measurements, mm: Holotype, male: body length 4.4; wing length 3.0, wing width 1.0; head width 0.7; preserved part of antenna 0.5. Additional specimens: body length, 3.8–3.9; wing length 1.9–2.4, wing width 0.7–0.9; head width 0.5–0.6; antenna length 0.9.

Remarks: In the holotype, only a short proximal portion of the antenna is visible—six more or less uniform flagellomeres—but its distal portion is poorly traceable, being obscured by a conchostracan carapace, so its complete length and the exact number and shape of flagellomeres are unknown (Figures 4c and 5d). The variability in the wing venation of male is recorded based on the two wings of the holotype (Figures 3, 4a,b and 5a,b). Variability in the wing venation of additional specimens—*m-cu* position at or just behind $M_{3+4}$ furcation, as well as ratio of the Rs stem/$R_{4+5}$ stem 1.0–1.5× and the basal portion of $M_{1+2}$ 6–10× as long as petiole—are found in two wings of one specimen SMNS-P-75643-4/5b (Figures 6f and 7a,b).

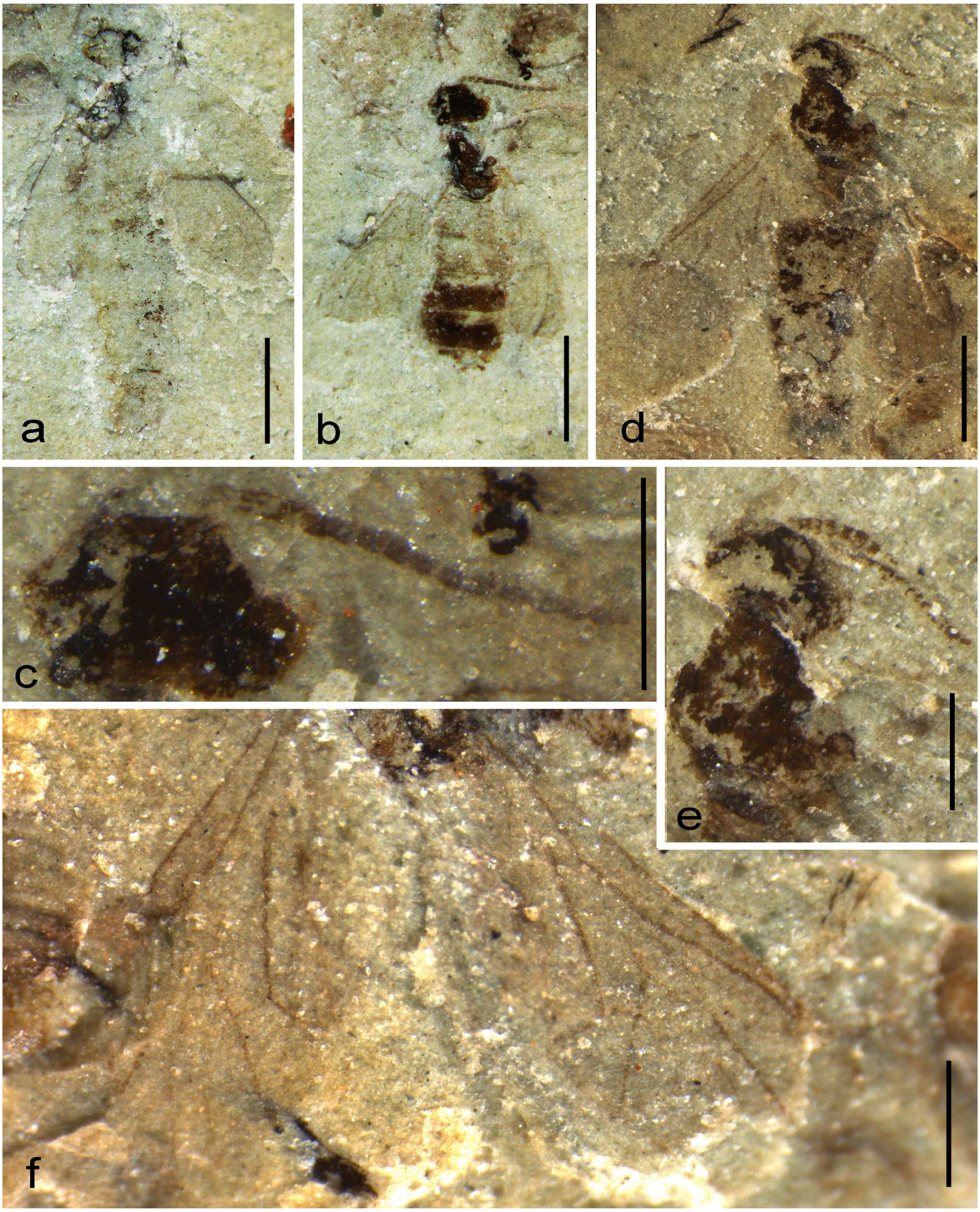

**Figure 6.** *Gallia alsatica* Krzemiński and Krzemińska, 2003, photographs. (**a**–**c**) SMNS-P-75643-4/5a, possibly female, total habitus, part and counterpart, head with antenna; (**d**,**e**) SMNS-P-75643-7, possibly female, total habitus, head with antennae; (**f**) SMNS-P-75643-4/5b, thorax with wings. Scale bars (**a**,**b**,**d**) 1 mm; (**c**,**e**,**f**) 0.5 mm.

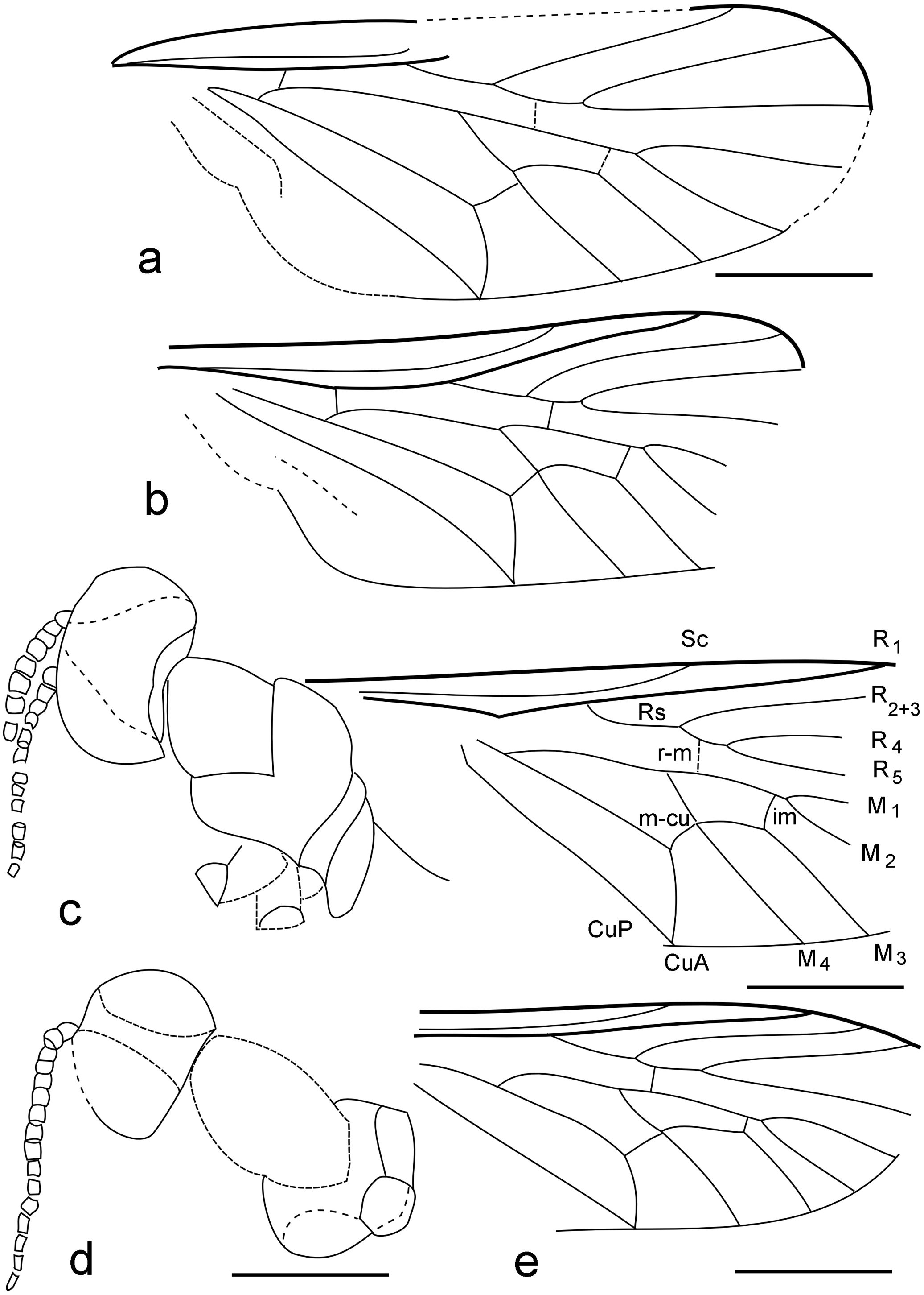

**Figure 7.** *Gallia alsatica* Krzemiński and Krzemińska, 2003, line figures. (**a**,**b**) SMNS-P-75643-4b, left and right wings; (**c**) SMNS-P-75643-7, possibly female, head with antennae, thorax and wing; (**d**,**e**) SMNS-P-75643-4a, possibly female, head with antenna and thorax, wing. Scale bars 0.5 mm.

## 4. Discussion and Conclusions

### 4.1. *Affinities of Vogerhyphus*

As demonstrated previously [8,14], Rs and M forks are usually shorter (with Rs origin and discal cell in the distal half of the wing) in the Triassic Tipulomorpha, so some characteristics of *Vogerhyphus* gen. nov. are tipulomorph. However, it is clear now that such tipulomorph proportions were common in Triassic members of Psychodomorpha, and no single proportion is sufficient to separate infraorders of Nematocera [2,18]. Therefore, the new subfamily possesses some peculiarities shared with Tipulomorpha and Psychodomorpha but it is attributed to the Mesozoic bibionomorph Prothorhyphidae based on the combination of the long but incomplete $A_1$, Rs pattern, M stem aligned with $M_{1+2}$, and *m-cu* position, whereas in extinct and living Anisopodidae, only the Rs pattern with three branches is distinct [19]. The $M_4$ bend on *m-cu* with an extremely short basal portion of $M_4$ is also known in extinct Hennigmatidae and extinct and extant Tanyderidae (Psychodomorpha *sensu* Hennig [20]), as well as *r-m* connecting the $R_5$ base; however, the combination of three Rs veins (with long unbranched $R_{2+3}$ not forming a stalk with $R_4$) and *m-cu* position is known only in the Prothorhyphidae.

In *V. blagoderovi*, CuA and CuP are clearly converging (but not meeting), so its brachyceran affinity cannot be entirely ruled out. In Brachycera, a similar pattern of media has been well-known to occur since the Triassic (*Gallia alsatica*); sometimes, the long $A_1$ is incomplete and cell *cua* is open. However, if CuA and CuP are converging but not meeting, as in some Rhagionidae and Bombyliidae, then the cross-vein *r-m* never connects at the $R_5$ base.

It is worth mentioning that in the Triassic stem-group of Brachycera, *Prosechamyia* Blagoderov and Grimaldi, 2007 from the Norian Cow Branch Formation of North America, veins of the radial sector are nearly straight and subparallel for most of their length. In addition, the $R_{4+5}$ stem is short and *r-m* connects the $M_{1+2}$ stem with the $R_5$ base, while the basal part of M is obvious and M is forking in the distal half of the wing [10], as in *Vogerhyphus* gen. nov. However, other characters of *Prosechamyia* are apomorphic: Sc and $R_1$ are shorter, the discal cell is absent, at least one or even two medial branches are lacking and cell *cua* is petiolate. Therefore, the protorhyphid affinity of *Vogerhyphus* gen. nov. seems to be more plausible at present.

### *4.2. Affinities of Gallia*

The genus *Gallia* was described as the oldest member of the Rhagionidae based only on its wing venation [7], with other features being left out of the discussion due to their unsatisfactory state of preservation in the only holotype.

The Rhagionidae are accepted as the basalmost—in both their morphology and their appearance in the fossil record—members of the Brachycera, with very few reliable adult synapomorphies [21,22]. Grimaldi and Cumming [23] suggested that the position of the $R_{4+5}$ fork is at the same level as the distal end of discal cell (and not distal to it) and the shape of $R_4$ (with a sharp bend at its base) and $R_5$ (straight) may work as synapomorphies for the majority of the Rhagionidae, but these characters demonstrate inter- and intrageneric variations [22]. Stuckenberg [21] considered $R_{2+3}$ with a distinct albeit moderate curvature beneath the stigma as one of autopomorphies of the Rhagionidae *s.str.* (i.e., after the exclusion of Austroleptidae and Spaniidae); other autapomorphies are in the female postabdomen and are generally unobservable in fossils. He also mentioned $R_4$ and $R_5$ enclosing the wing apex as an additional character for the family, but this also occurs in the Athericidae and Tabanidae. Shcherbakov et al. [14] used another set of characters for the Rhagionidae and Xylophagidae *s.l.* (including *Protobrachyceron* Handlirsch, 1920) when they discussed the systematic position of the Late Triassic Alinkidae: (1) Rs originating well before the M fork; (2) Rs forking level with the M fork; (3) Rs not aligned with $R_{4+5}$ and bent at *r-m*; (4) cell *r*3 at least as broad as *r*5; and (5) *m-cu* joining CuA far beyond its midlength and $M_{3+4}$ close to $M_{3+4}$ fork, or $M_4$. However, these characters cannot be considered autapomorphies or synapomorphies of the Rhagionidae and Xylophagidae, for they are also found, either isolated or in combination, in the Protorhyphidae or other nematoceran taxa.

Although the inclusion of *Gallia* in the Rhagionidae was somewhat acceptable at the time of its original description, its actual existence among the snipe flies seems contentious in light of information derived from the wing venation. In this Triassic genus (Figure 5a,b), $R_{2+3}$ has no curvature beneath $R_4$, the $R_{4+5}$ fork is noticeably proximal to the distal end of discal cell, $R_4$ has no sharp bend at its base but is instead gently curved, and $R_5$ does not actually form a continuous line with the $R_{4+5}$ stem (and Rs). Thus, none of the presumed rhagionid apomorphies are found in the wing venation of *Gallia*. It should be noted that some Early Jurassic genera described from isolated wings were attributed to the Rhagionidae despite having a straight $R_{2+3}$. These are *Grimmyia* Ansorge, 1996 [16], *Liassobrachyceron* Krzemiński and Ansorge, 2005 [24] and *Taschigatra* Mostovski and Jarzembowski, 2000 [25]. The last genus was placed into the Rhagionidae not without some doubt, and all three may actually belong in the Xylophagidae, along with Early–Late Jurassic *Protobrachyceron*, whose species are known from both wings (Germany, $J_1$ [26,27]) and complete bodies (China, $J_2$ [28]), including stylate antennae (Kazakhstan, $J_2$–$J_3$; MBM unpubl. data).

The genus displays another peculiarity by having the *im* crossvein proximal of the $M_{1+2}$ fork. A similarly stalked $M_{1+2}$ fork crops out in several extant and extinct genera of the Rhagionoidea *sensu* Kerr [22]—*Alloleptis* Nagatomi and Saigusa, 1982 (Recent), *Omphalophora* Becker, 1900 (Recent), *Paleochrysopilus* Grimaldi and Cumming, 1999 (Lebanese amber, $K_1$ [23]) and *Ptiolinites* Kovalev, 1986 (Mongolia, Russia, Spain, UK, $K_1$ [29,30])—as well as in quite a few extinct and extant representatives of nematoceran and brachyceran families, e.g., Apystomyiidae, Cramptonomyiidae, Empididae, Limoniidae, Nadipteridae, Protorhyphidae, Ptychopteridae, Rhagionemestriidae, Uranorhagionidae *etc*., so this character is not unique to the snipe flies.

A re-examination of the holotype and the discovery of additional specimens of *G. alsatica* in the Grauvogel's collection further complicated the conundrum of the systematic position of the genus *Gallia*. The holotype of *G. alsatica* demonstrated structures adjacent to the head that can be interpreted as six subequal segments of the flagellum, which distal part is hidden under a conchostracan carapace (Figures 3a, 4c and 5d). Two additional specimens (possibly females) with nearly identical wing venation compared to the holotype, have long moniliform antennae with 16 almost uniform segments preserved in one of them (Figures 6b–e and 7c,d). Such antennae with a small and subequal scape and pedicel and 14 more or less uniform flagellomeres are unknown in virtually any Brachycera, whose fundamental distinguishing characteristic is an antenna with a maximum of eight flagellomeres [31].

Hennig [32] proposed that a distinct separation of the first flagellomere from the rest of the flagellum could be a synapomorphy for the Rhagionidae, whereas Stuckenberg [31] saw the progressive fusion of flagellomeres into an enlarged flagellar base as a synapomorphy of all Brachycera. In the Stratiomyidae, the unfused basal segments of the flagellum may form a morphologically compact unit that looks like a single stoutly rounded segment [33]. However, there is no rule without an exception. The members of the family Rachiceridae possess from 14 to up to over 30 flagellomeres in a pectinate, serrate or moniliform antenna [34], but the Rachiceridae have a far more advanced wing venation compared to Galliidae, with a strongly curved $R_1$, much shorter fork $R_{4+5}$ and closed *m3* cell. On the other hand, similar antennal structures appear in some Nematocera. The antenna of the bibionomorph *Burmazelmira aristica* Grimaldi, Amorim and Blagoderov, 2003 (Archizelmiridae; Myanmar, $K_2$) has a 12-segmented structure [35] (p. 379, Figures 10-2, 10-3) that superficially resembles the enlarged first segment of the postpedicel in the Stratiomyidae. The differentiation of flagellomeres in this and two other genera of the Archizelmiridae was one of the reasons why they were placed in a separate subfamily Burmazelmirinae [36]. Further examples of brachycera-type antenna are provided by *Burmahesperinus* Ševčík, Skartveit, Krzemiński and Skibińska, 2021 (Bibionidae [37]), also from the Cretaceous amber of Myanmar. Two species of this bibionid genus have 10–12-segmented flagella with enlarged basal flagellomeres, one species has a 12-segmented flagellum with a slightly enlarged basal segment but greatly swollen pedicel, and the fourth species has a 6-segmented flagellum with a terminal bristle and an enlarged basal part formed by two closely attached but unfused segments. The Late Triassic *Alinka cara* Krzemiński, 1992—originally described as Brachycera in a family of its own [38]—has a 10-segmented antenna, but its submoniliform flagellum is more consistent with nematoceran affinities of the genus, and it is now considered a member of Procramptonomyiidae [10,14,31].

With its moniliform antenna comprising 14 practically uniform flagellomeres, *G. alsatica* not only completely ruins the feeble integrity of the Rhagionidae if added to the family, but also does not fit into the Brachycera altogether. The only taxa with a brachycera-type wing venation (i.e., closed *cua* cell) that might have antennae resembling those of *G. alsatica* are *Prosechamyia dimedia* Blagoderov and Grimaldi, 2007 and, to some extent, *Prosechamyia trimedia* Blagoderov and Grimaldi, 2007 (Prosechamyiidae) from the Norian of the USA [10]. Regrettably, the antennae are incompletely preserved in both prosechamyiids, which were left unassigned as the stem-group for all Brachycera based on a unique combination of wing and antennal characters. We are tempted to follow suit, but would like to emphasize the possible affinity of the Galliidae with Protorhyphidae, with the latter being thought of as ancestral to the Brachycera [14,39]. Veins CuA and CuP demonstrate a trend towards convergence in some Protorhyphidae, e.g., in *Vogerhyphus* gen. nov., yet cell *cua* remains open in protorhyphids.

The progressive changes in the dipteran antenna towards a reduction in the number of segments and, more importantly, towards the differentiation of flagellomeres bearing chemo- and mechanoreceptors, is a pivotal point in the evolution of the order during the Triassic and Jurassic [31], probably more important than the closure of the *cua* cell, which may be linked to the geometry of the wing. Stuckenberg [31] hypothesized that the origin of the Brachycera was prompted by a new feeding mode, which manifested in the concomitant appearance of the modified antenna and enlarged labella, like those in, for example, Jurassic *Paleobrachyceron* Kovalev, 1981 (Russia, $J_1$–$J_2$ [40]), *Palaeoarthroteles mesozoicus* Kovalev and Mostovski, 1997 (Russia, $J_3$ [41]), *Protorhagio karataviensis* Mostovski, 2008 and *Protorhagio ponomarenkoi* Mostovski, 2008 (Kazakhstan, $J_2$–$J_3$ [42]). A discovery of two archizelmirids [35]—*Zelmiarcha lebanensis* Grimaldi, Amorim and Blagoderov, 2003 (Lebanon, $K_1$), with unmodified flagellum and small labella, and *Burmazelmira aristica* Grimaldi, Amorim and Blagoderov, 2003 (Myanmar, $K_2$), with heavily modified flagellum and enlarged labella (see above)—supports Stuckenberg's hypothesis of the concurrent appearance of the two characters, but also shows that such a trait might have appeared in a group unrelated to the Brachycera. Labandeira [43,44] noted that the early Mesozoic was the time when one of the major diversifications of insect—and Diptera in particular—mouthparts happened.

Budd and Jensen [45] and Stuckenberg [21] highlighted that the last common ancestor of any two clades cannot have the body plan of either of them and may not be readily recognizable in the palaeontological record. In other words, the clades split before they could be recorded as fossils. The two characters—the closed *cua* cell and the eight-segmented antennal flagellum with differentiated basal flagellomeres—that unite the Brachycera, did not appear simultaneously in the stem group comprising Prosechamyiidae and Galliidae, but developed separately in time. Moreover, other 'attempts' to develop 'brachyceran' lineages based on a similar modification of the antennae cropped out in the Cretaceous members of the families Archizelmiridae [35] and Bibionidae [37]. This process can be called brachycerization, akin to other '-izations' (e.g., arthropodization, tetrapodization, reptilization, ornithization, angiospermization, etc.), which resulted in major evolutionary changes [46].

Both Prosechamyiidae and Galliidae probably belonged to a group that can be jokingly (and oxymoronically) dubbed nematocerous brachycerans, whose representatives with eight-segmented flagellum and differentiated basal flagellomeres will never be found, for they would be seen as the true Brachycera.

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