



New subgenus and two new species of the genus *Palaeoglaesum* and its position within Bruchomyiinae (Psychodidae)

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Abstract. Phylogenetic analyses between fossil species of the subfamily Bruchomyiinae were conducted. Based on them, a new subgenus, *Palaeoglaesum* (*Amplissimum*) subgen. nov., within the genus *Palaeoglaesum* is proposed. Two new species, *Palaeoglaesum angustum* sp. nov. and *Palaeoglaesum cracoviae* sp. nov., from Cretaceous Myanmar amber are described and illustrated herein.

Key words: moth fly, taxonomy, fossil insects, inclusions, Mesozoic, phylogeny.

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I. INTRODUCTION

Psychodidae NEWMAN, 1834 (commonly named sand flies, moth flies or drain flies) is a morphologically and systematically diverse family of Diptera with a worldwide distribution. There are six extant subfamilies – Bruchomyiinae ALEXANDER, 1920; Horaiellinae ENDERLEIN, 1936; Phlebotominae RONDANI, 1840; Psychodinae NEWMAN, 1834; Sycoracinae RONDANI, 1856; and Trichomyiinae TONNOIR, 1922 – and one extinct subfamily, i.e. Datziiinae STEBNER, SOLORZANO-KRAEMER, IBÁÑEZ-BERNAL & WAGNER, 2015 (in STEBNER et al. 2015b; replacing Protopsychodinae STEBNER et al. 2015a). Immature specimens are often associated with moist (springs and streams) or foul habitats (drains and sewage). They can also be observed in terrestrial habitats, mainly in saturated rotting wood and moist leaf litter. Adults are characterised by their small size (1-5 mm) and

heavily setose bodies, which superficially resemble those of moths.

The majority of species are harmless and have no effect on humans (CURLER and MULTON 2012; FAIRCHILD 1952; HANSON 1968; WAGNER and STUCKENBERG 2012). However, some adult species of Phlebotominae are of medical importance, because they feed on blood and may spread diseases (leishmaniasis, or sandfly fever) to humans and animals (LEWIS et al. 1977). Moreover, some Psychodinae species cause myiasis infections in humans (RIEGEL and KNISKERN 1963; CURLER and MULTON 2012).

In the fossil record, the family Psychodidae is undoubtedly known from the Lower Jurassic (ANSORGE 1994), although BLAGODEROV et al. (2007) states that it evolved as early as the Triassic. However, the taxonomic classification of the described materials to this understudied family is questionable (SKIBIŃSKA et al. 2019). The fossil record of Psychodidae

is essential for retracing essential morphological homologies, thereby enabling us to observe the patterns of diversification and establish phylogenetic relationships.

The subfamily Bruchomyiinae currently includes less than 60 species, distributed in tropical and subtropical regions (CURLER and JACOBSON 2012; WAGNER and STUCKENBERG 2016; WAGNER 2017). It is comprised of seven extant genera – *Alexandria* WAGNER & KVIFTE 2018 in POLSEELA et al. (2018); *Boreofairchildia* WAGNER & STUCKENBERG, 2016; *Bruchomyia* ALEXANDER, 1920; *Eutonnoiria* ALEXANDER, 1940; *Laurenceomyia* WAGNER & STUCKENBERG, 2016; *Nemopalpus* MACQUART, 1838; and *Notofairchildia* WAGNER & STUCKENBERG, 2016 – and four extinct genera, i.e. †*Hoffeinsodes* WAGNER, 2017; †*Libanonemopalpus* AZAR, SZWEDO & MAKSOUD, 2022 (in AZAR et al. 2022); †*Palaeoglaesum* WAGNER, 2017; and †*Palaeosycorax* MEUNIER, 1905. Throughout this study, we maintain the system of taxonomic classification of fossil Bruchomyiinae proposed by WAGNER (2017), where †*Palaeosycorax* is treated as a separate genus and is not synonymous with *Nemopalpus* as was suggested by EVENHUIS (1994).

Bruchomyiinae arouses great interest among dipterists and is often referred to as the ‘most plesiomorphic’ group among Psychodidae (SANTOS et al. 2009; WAGNER and STUCKENBERG 2012; WAGNER 2017). However, as was discussed in SKIBIŃSKA et al. (2019), this ‘is irrelevant to the phylogenetic placement of this or any group, as it is impossible to determine relationships based on plesiomorphies. Nonetheless, it is helpful to evaluate the character polarity in a given taxon, and the fossil specimens of Bruchomyiinae allow for this’. A first fossil of the Bruchomyiinae, *Palaeosycorax tertiariae* (MEUNIER, 1905), was described from Baltic amber and was originally classified in Psychodidae. However, ALEXANDER (1920) described the genus *Bruchomyia*, for which he established a new subfamily Bruchomyiinae in the Tanyderidae, which was transferred by EDWARDS to Psychodidae (EDWARDS, 1921). A detailed taxonomic history of the subfamily Bruchomyiinae was provided by WAGNER (2016). Currently, we recognise 27 fossil species belonging to the studied subfamily (Table 1), all of which are described from fossil resins. It seems that the greatest diversity of Bruchomyiinae is found in Cretaceous Burmese amber (KS: unpublished data). However, this subfamily is represented by only one genus, i.e. *Palaeoglaesum* WAGNER, 2017, which consists of 13 species described to date.

In this article we provide a description of two new species of the fossil genus *Palaeoglaesum*. Moreover, we provide detailed documentation and an additional description for three species that were previously described, i.e. *Palaeoglaesum bisulcum* WAGNER, 2017, *Palaeoglaesum notandum* WAGNER, 2017 and *Palaeoglaesum mulleri* WAGNER, 2017. After an examination of specific character states in the head, wing and male genitalia, a phylogenetic analysis was performed, on the grounds of which we propose distinguishing a new subgenus within the genus *Palaeoglaesum*, *Palaeoglaesum (Amplissimum)* subgen. nov.

II. MATERIAL AND METHODS

Specimen and media repositories. The amber specimens included in this study were collected in Myanmar before 2017, and are currently held in the collections of the Natural History Museum of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland, ISEA PAS (MP).

Specimen observation, measurements and illustration. All of the amber pieces were cut and polished with sandpaper of different grain sizes and polishing paste, to attain the optimal visibility of the specimens. The examinations and measurements of the fossil specimens were completed using a Nikon SMZ25 stereomicroscope, equipped with a Nikon DS-Ri2 digital camera. Measurements are given in millimetres. The wing length was measured from the base of the alula to the wing apex; while the wing width was measured at the point of greatest distance between the anterior and posterior wing margins. Photomicrographs of the specimens are focus stacks and were combined using NIS-Elements Imaging Software. The line drawings were initially based on traced photos, with edits for accuracy according to direct specimen observations. The photomicrographs were optimised for colour balance and clarity using Adobe Photoshop® CS6; while the vector line drawings and figure plates were prepared using Adobe Illustrator® CS3.

Descriptive terms. The general morphology and use of terms follow CUMMING and WOOD (2017), except for the interpretation of the wing veins, which is that of KRZEMIŃSKI and KRZEMIŃSKA (2003).

Locality. The specimens included in this study come from northern Myanmar, Hukawng Valley in Kachin Province (KANIA et al. 2015: Fig. 1). In the mid-Cretaceous period, the Myanmar amber palaeogeographical locality was quite near to the equator

(YIN et al. 2018: fig. 1b). Based on radiometric date obtained from the amber bearing sedimentary rock, the geological age of the Myanmar amber is considered to be the earliest Cenomanian, about 99 Ma (SHI et al. 2012; SMITH and ROSS 2016; YU et al. 2019).

Phylogeny. The phylogenetic matrix was built using WinClada software (NIXON 2002). Missing states were scored with '?' and inapplicable states with '-'. The phylogenetic analysis was done using TNT 1.5 software (GOLOBOFF et al. 2016) under the criterion of parsimony with Implicit Weighting (GOLOBOFF 1993). All characters were treated as unordered. The analysis was done using heuristic searches with tree-bisection reconnection (TBR) branch swapping, with 1,000 replicates holding up to 100 trees per replication.

This published work and the nomenclatural acts it contains have been registered in ZooBank. The LSID for this publication is: urn:lsid:zoobank.org:pub:91CA5798-DD85-41F3-83CB-A244209686B9.

III. RESULTS

Systematic palaeontology

Order **Diptera** LINNAEUS, 1758

Family **Psychodidae** NEWMAN, 1834

Subfamily **Bruchomyiinae** ALEXANDER, 1920

Genus ***Palaeoglaesum*** WAGNER, 2017

Subgenus ***Palaeoglaesum (Palaeoglaesum)***
WAGNER, 2017

Type species *Nemopalpus quadrispiculatus* STEBNER, SOLÓRZANO-KREMER, IBÁÑEZ-BERNAL and WAGNER, 2015a: 22, figs. 14 a, b, c, d. Myanmar amber; earliest Cenomanian (Cretaceous), by original designation.

The species, all from Burmese amber, included: *Palaeoglaesum bisulcum* WAGNER, 2017; *P. carsteni* SKIBIŃSKA, KRZEMIŃSKI & ZHANG, 2019; *P. gregi* SKIBIŃSKA & KRZEMIŃSKI, 2023; *P. jakubi* SKIBIŃSKA, 2023; *P. mulleri* WAGNER 2017; *P. myanmari* SKIBIŃSKA, 2023; *P. notandum* WAGNER, 2017; *P. pilosus* SKIBIŃSKA, KRZEMIŃSKI & ZHANG, 2021; *P. quadrispiculatum* STEBNER, SOLÓRZANO-KREMER, IBÁÑEZ-BERNAL, WAGNER, 2015; *P. stebneri* SKIBIŃSKA & KRZEMIŃSKI 2021; *P. teres* SKIBIŃSKA & ALBRYCHT 2021; *P. velteni* WAGNER, 2012; and *P. wagneri* SKIBIŃSKA, KRZEMIŃSKI & ZHANG, 2019.

Diagnosis. As in SKIBIŃSKA et al. (2019: 3).

Remarks. Species included in the subgenus *Palaeoglaesum (Palaeoglaesum)* are characterised by male genitalia with the aedeagus elongate, noticeably longer than wide (more than five times), bent toward the gonopods, always with a bifurcate apex; aedeagus is surrounded basally by a sleeve-like parameral sheath.

Palaeoglaesum (Palaeoglaesum) muelleri
WAGNER, 2017, comb. nov.

Fig. 1

Description. See WAGNER, 2017:114-115, figs. 7a-c

Remarks. WAGNER (2017) provided a detailed description of *P. muelleri*; however, the original publication lacked photographic documentation and a detailed drawing of the male's genitalia, which we present herein (Fig. 1). An additional examination of the specimen revealed that the gonostylus is broad and rounded at the basal part, smoothly tapering by approximately half at about one-quarter of its length, clearly curved well beyond half of its length, and rounded at the end (Figs 1c, f).

Palaeoglaesum (Palaeoglaesum) notandum
WAGNER, 2017, comb. nov.

Fig. 2

Description. See WAGNER, 2017:117-118, fig. 7e (wrongly labelled in the original figure caption as 'd').

Amended description of wing. End of Sc well before fork of R_{4+5} into R_4 and R_5 and before fork of M_{1+2} into M_1 and M_2 ; sc-r slightly more than its length before end of Sc; R_1 waved at end, joining C in about 5/6 of R_2 and proximal to level of end of M_1 ; Rs short, less than half length of R_{4+5} ; R_{2+3} slightly longer than R_2 and 2x longer than R_{4+5} ; R_4 3x as long as R_{4+5} and as long as R_5 ; M_{1+2} slightly more than 7x as long as M_{3+4} ; m-cu situated between M_4 and Cu about half its length beyond fork of M_{3+4} into M_3 and M_4 , and 6x its length from end of Cu; opening of m4 cell only slightly wider than opening of cu cell (Figs 2a, b).

Remarks. The specimen is completely preserved in a light-coloured amber piece containing many air bubbles. However, about one-third of the holotype's length runs through a crack, which partially hinders an analysis and makes the specimen likely to split apart. The holotype was protected by making a slide in Canadian balm. Additional analyses allowed us to reconstruct details in the wing venation pattern.

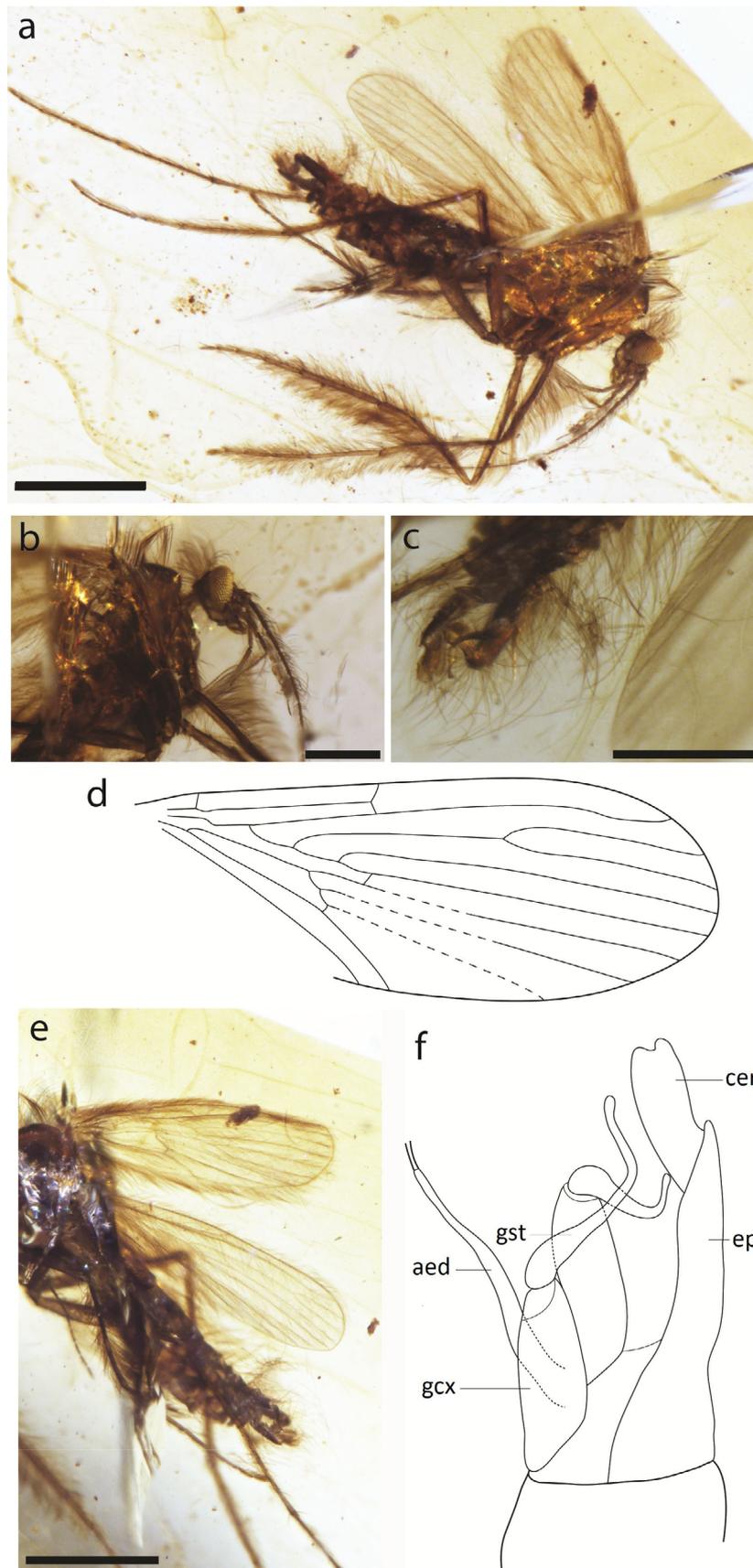


Fig. 1. Photos and drawings of *P. muelleri*: a – habitus of holotype; b – head and thorax; wing; c – male genitalia; d – interpretative line drawing of wing; e – wing and abdomen; f – interpretative line drawing of male genitalia. Abbreviations: aed, aedeagal complex; cer, cerci; ep, epandrium; gcx, gonocoxite; gst, gonostylus. Scale bars [mm]: a – 1; b – 0.5; c – 0.5; e – 1.

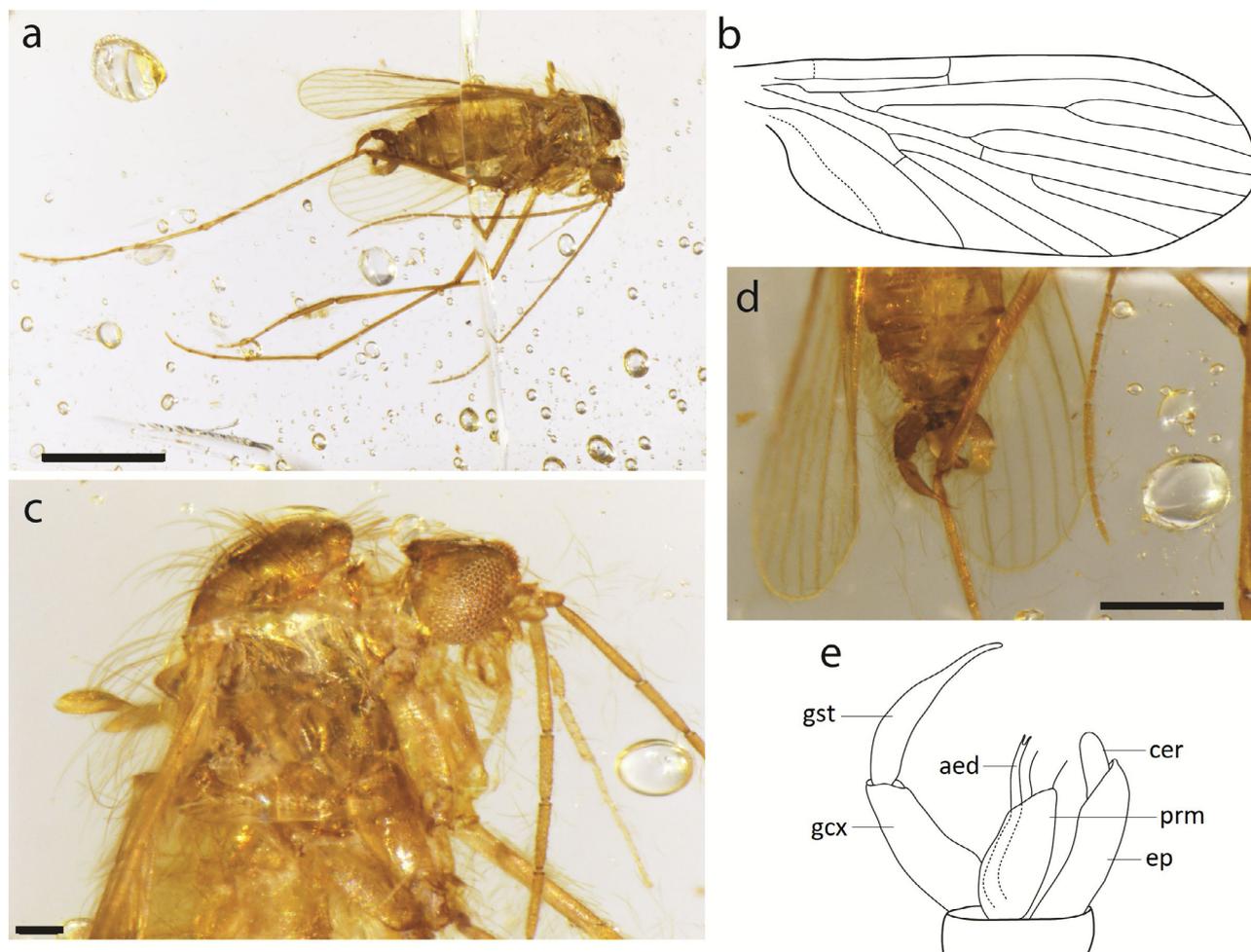


Fig. 2. Photos and drawings of *P. notandum*: a – habitus of holotype; b – interpretative line drawing of wing; c – head and thorax; d – male genitalia; e – interpretative line drawing of male genitalia. Abbreviations as in Fig. 1. Scale bars [mm]: a – 1; c – 0.1; d – 0.5.

***Palaeoglaesum (Palaeoglaesum) cracoviae* sp. nov.**
SKIBIŃSKA

Fig. 3

LSID urn:lsid:zoobank.org:act:46307978-8829-4521-B420-1847DDCDA29C

Diagnosis. A *Palaeoglaesum* species with elongated, narrow gonocoxite, longer than gonostylus by about one-third of its length; gonostylus long and slender, rounded in basal part, with brush of robust bristles at its base, significantly bent at about 3/4 of its length; end tapered and rounded.

Etymology. The specific epithet refers to the name of the Polish city of Kraków, the former capital of Poland, where the research on the Psychodomorpha fossil is being performed.

Description. Wing: length 1.78 mm; width 0.68 mm.

Head partially preserved; antennae with fourteen elongate, cylindrical flagellomeres tapering and con-

siderably reducing in size distad; all covered with long bristles; scapus and pedicel not visible; labelum elongated, with mouthparts not clearly visible; palps elongate, with five segments, basal segment inconspicuous, last segment elongated nearly as long as all preceding segments combined (Figs 3a, b, c).

Wing heavily setose; setation dense and longer in basal part, especially along lower wing margin; end of Sc well beyond fork of R_{4+5} into R_4 and R_5 and slightly before fork of M_{1+2} into M_1 and M_2 ; sc-r at about its length before end of Sc; R_1 elongate, bent upwards at end, joining C in about 1/3 length of R_2 and almost opposite end of M_1 ; Rs about 1 3/4 x as long as R_{4+5} ; R_{2+3} 2x as long as R_2 and 4.5x longer than R_{4+5} ; R_4 6x as long as R_{4+5} and nearly as long as R_5 ; M_{1+2} almost 4.5x as long as M_{3+4} ; m-cu situated between M_4 and Cu about half its length beyond fork of M_{3+4} into M_3 and M_4 , and 4.5x its length from end of Cu; opening of m4 cell about 2x longer than opening of cu cell (Figs 3a, d, e).

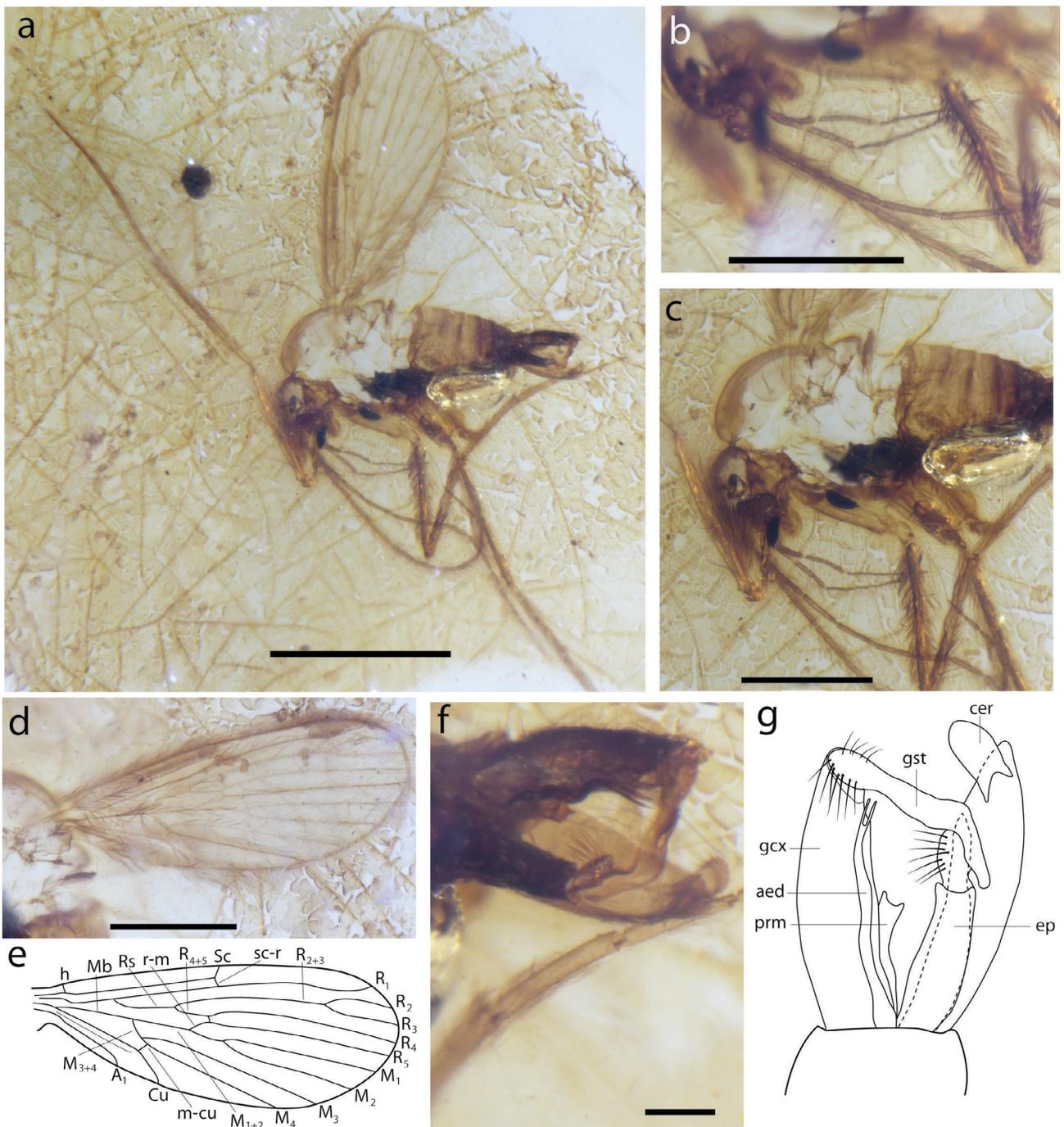


Fig. 3. *Palaeoglaesum (Palaeoglaesum) cracoviae* sp. et subgen. nov., holotype MP/4572, a – habitus of holotype; b – head with antenna and palpi; c – head and thorax; d – wing; e – interpretative line drawing of wing; f – male genitalia; g – interpretative line drawing of male genitalia. Abbreviations as in Fig. 1. Scale bars [mm]: a – 1; b – 0.1; c – 0.1; d – 0.5; f – 0.1.

Legs covered with long setation (Figs 3a, b).

Abdomen. Gonocoxite elongated and narrow (about 0.35 mm long and 0.1 mm wide), longer than gonostylus by about 1/3 of its length; gonostylus long and slender, rounded in basal part, with a set of robust bristles at its base, significantly angled downwards at about 3/4 of its length, end tapered and

rounded (Figs 1f, g); aedeagus elongated, sigmoidal, bent toward gonopods, apex bifurcated.

Material examined. Holotype MP/4572, male; preserved in Myanmar amber (earliest Cenomanian, 98.79 ± 0.62 Ma), deposited in the collection of the ISEA PAS.

Female unknown.

Remarks. The specimen is preserved in the amber piece with numerous infiltrations and contaminations through which detailed observations and, in particular, taking photographs is possible mainly from one side. The head and thorax are poorly preserved. However, all significant diagnostic features on the structure of the male genitalia are clearly visible.

***Palaeoglaesum (Palaeoglaesum) angustum* sp. nov.**
SKIBIŃSKA & SANTOS

Fig. 4

LSID urn:lsid:zoobank.org:act:E0BCEB1A-7DD1-4E0B-8B21-E1BC5CDC68FC

Diagnosis. A *Palaeoglaesum* species with gonocoxite slender and elongated, slightly broader in middle part; gonostylus significantly elongated, twice as long as gonocoxite, abruptly narrowed at mid-length, forming a thin, curved appendage longer than basal one; basal part covered with numerous long bristles.

Etymology. The specific epithet refers to the structure of the gonocoxites, which are greatly elongated (Latin, gender neutrum: angustum = narrow).

Description. Wing: length 2.02 mm; width 0.72 mm.

Head. Antennae well preserved, with fourteen elongate-cylindrical flagellomeres, with narrow ends, reducing in size distad, all covered with long bristles, particularly dense on first five flagellomeres; scapus not well visible, pedicel elongated, wide and oval; labellum elongated; palps long and thin, with five segments, basal segment inconspicuous, last palpomere longer than all preceding segments combined (Figs 4a, b).

Thorax. Wing veins heavily setose, hairs dense and longer in basal part; end of Sc well behind fork of R_{4+5} into R_4 and R_5 almost in middle of M_{1+2} ; sc-r about its length before end of Sc; R_1 slightly bent upwards at end, joining C beyond half of R_2 and almost opposite end of M_2 ; Rs about 2x as long as R_{4+5} ; R_{2+3} slightly longer than 2x R_2 and about 4.5x longer than R_{4+5} ; R_4 slightly more than 6x R_{4+5} and nearly as long as R_5 ; M_{1+2} almost 5x as long as M_{3+4} ; m-cu situated between M_4 and Cu, slightly beyond fork of M_{3+4} into M_3 and M_4 and slightly longer than 3x its length from end of Cu (Fig. 4e); opening of m4 cell about 3x longer than opening of cu cell (Figs 4a, d, e).

Legs covered with setae.

Abdomen. Gonocoxite slender and elongated (0.24 mm long), slightly broader in middle part; gonostylus greatly elongated, almost twice as long

as gonocoxite, abruptly narrowed at mid-length (in about 0.22 mm), forming a thin, curved appendage longer than basal portion (0.20 mm long); basal part covered with numerous long bristles; aedeagus long, bent toward gonopods, apex bifurcated (Figs 4 c, f).

Material examined. Holotype MP/4571 – male; preserved in Myanmar amber (earliest Cenomanian, 98.79 ± 0.62 Ma), deposited in the collection of the ISEA PAS.

Female unknown.

Remarks. The holotype is preserved in highly contaminated amber, containing a large amount of organic matter with a lot of cracks, which makes a photographic documentation very difficult. Specimen is well preserved; however, one wing is folded.

Subgenus *Palaeoglaesum (Amplissimum)*
subgen. nov. SKIBIŃSKA

Diagnosis. New subgenus differs from *Palaeoglaesum (Palaeoglaesum)* by an aedeagus not bifurcated, broad and short, significantly shorter than the parameral sheath.

Etymology. The subgeneric epithet refers to the shape of the aedeagus, which is significantly wider than the parameral sheath, not bifurcated and wide. (Latin, gender neutrum: amplissimum = widest).

Type species: *Palaeoglaesum (Amplissimum) bisulcum* (WAGNER, 2017), comb. nov. By monotypy, the description of the genus is the same as that of its only species.

Palaeoglaesum (Amplissimum) bisulcum
WAGNER, 2017, comb. nov.

Fig. 5

Description. As in WAGNER, 2017:117, fig. 7d (wrongly labelled in the original figure caption as 'e')

Remarks. The specimen is preserved right at the edge of the amber piece (Fig. 5a), which makes it impossible to reconstruct the wing venation pattern, although various observation techniques were used. The holotype has features typical for the genus, where the distinctive arrangement of the bristles on the legs and head can be noticed at first sight (Figs 5a, b, c). After a thorough analysis of the details of the male genitalia, it was observed that the aedeagus is short and not bifurcated (Fig. 5d, e), which is inconsistent with the features of the genus *Palaeoglaesum*. The phylogenetic analysis (Fig. 6) performed also indicated that *Palaeoglaesum bisulcum* definitely belongs to the genus; however, forming a sister group to all the other species. Considering the result of the phylogenetic analyses and morphological comparisons, we propose distinguishing

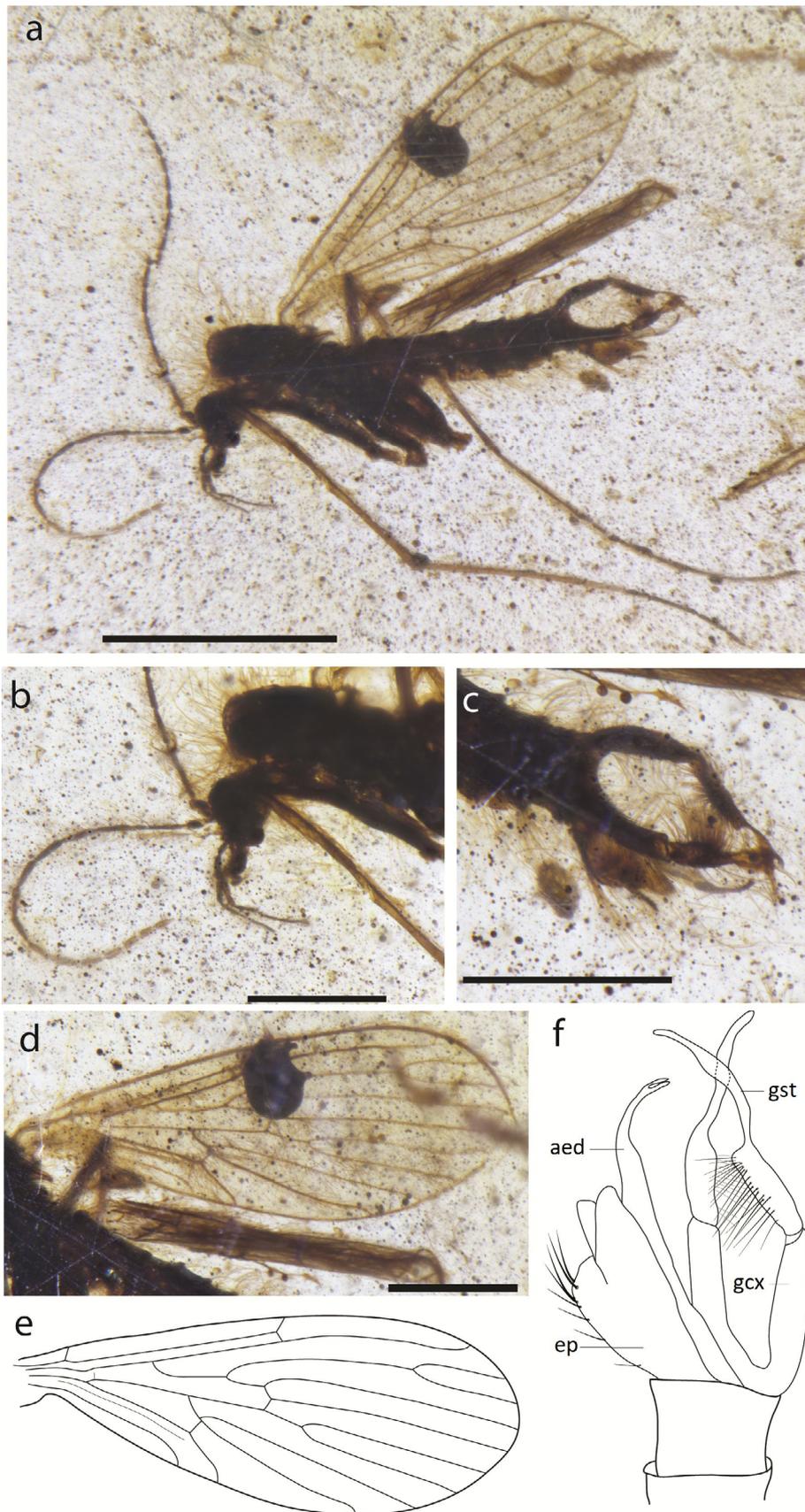


Fig. 4. *Palaeoglaesum (Palaeoglaesum) angustum* sp. nov., holotype MP/4571, a – habitus of holotype; b – head with antenna and palpi; c – male genitalia; d – wing; e – interpretative line drawing of wing; f – interpretative line drawing of male genitalia. Abbreviations as in Fig. 1. Scale bars [mm]: a – 1; b – 0.5; c – 0.5; d – 0.5.

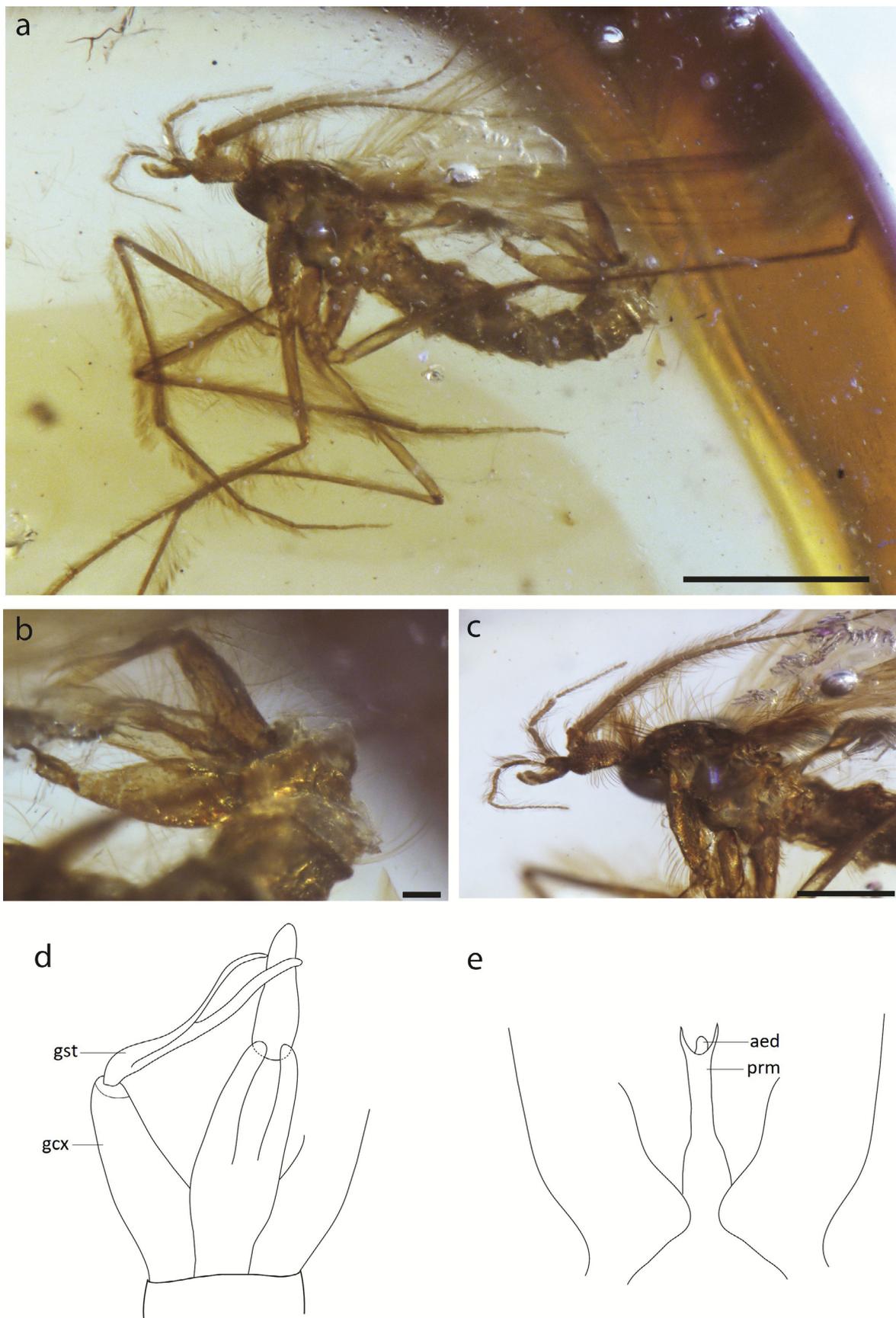


Fig. 5. Photos and drawing of *Palaeoglaesum (Amplissimum) bisulcum* comb. nov. a – habitus of holotype; b – male genitalia; c – head and thorax; d, e – interpretative line drawing of male genitalia. Abbreviations as in Fig. 1. Scale bars [mm]: a – 1; b – 0.1; c – 0.1.

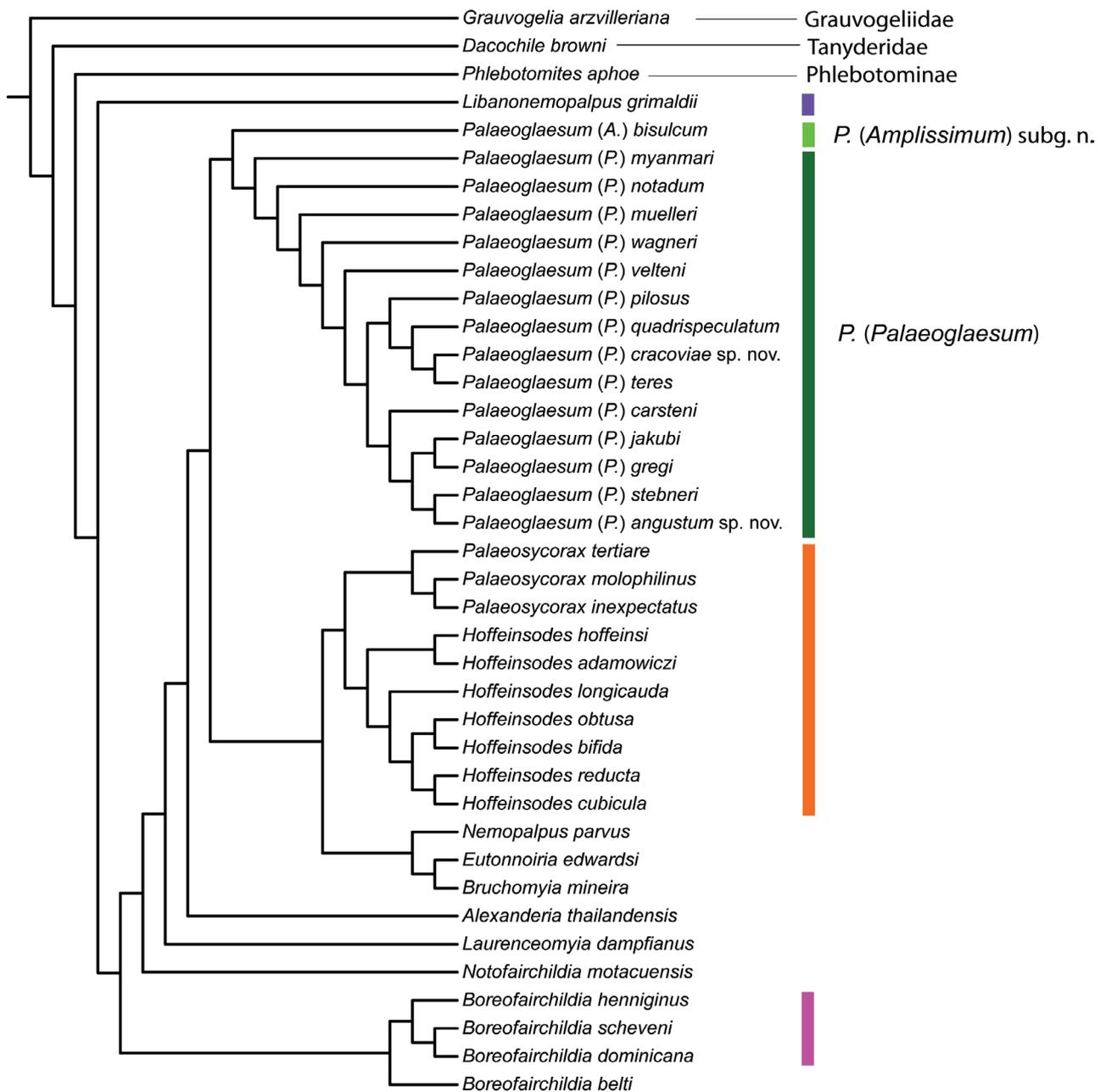


Fig. 6. Phylogeny of Bruchomyiinae evidencing the two subgenera of *Palaeoglaesum*. Extinct lineages are evidenced: in violet – Lebanese amber; in light and dark green – Burmese amber; in orange – Baltic amber; in purple – Dominican amber.

a new subgenus within the genus *Palaeoglaesum* i.e., *Palaeoglaesum (Amplissimum)*. With the appearance of new, better-preserved material, perhaps it will be possible to establish a new genus in the future; at present, we consider this premature.

IV. PHYLOGENY

The analysis included both fossil (Table 1) and contemporary species, i.e.: *Alexanderia thailandensis* POLSEELA, WAGNER, KVIFFTE, RULIK & APIWATHNISORN,

2018 (POLSEELA et al. 2018); *Bruchomyia mineira* BRAVO & BARATA, 2012; *Eutonnoiria edwardsi* TONNOIR, 1939; *Laurenceomyia dampfianus* ALEXANDER, 1940; *Nemopalpus parvus* SANTOS, FALQUETO & BRAVO, 2013; *Notofairchildia motacuensis* JEŽEK, OBOŇA & LE PONT, 2018 (in JEŽEK et al. 2018); and *Boreofairchildia belti* JEŽEK, OBOŇA & LE PONT, 2018 (in JEŽEK et al. 2018). The characters we used are listed below and the matrix of characters is presented in Table 2. The character states are based on original species descriptions (references are listed in Table 1).

Table 1

Fossil species belonging to subfamily Bruchomyiinae. * in SKIBIŃSKA et al. (2019); ** in SKIBIŃSKA et al. (2021); *** in SKIBIŃSKA et al. (2023); **** in AZAR et al. (2022)

Species	Locality
<i>Boreofairchildia dominicana</i> WAGNER, 2017	Dominican amber (Miocene)
<i>Boreofairchildia hennigianus</i> (SCHLÜTER, 1978)	Dominican amber (Miocene)
<i>Boreofairchildia scheveni</i> (WAGNER, 2006)	Dominican amber (Miocene)
<i>Palaeosycorax inexpectatus</i> WAGNER, 2012	Baltic amber (Eocene)
<i>Palaeosycorax molophilinus</i> (EDWARDS, 1921)	Baltic amber (Eocene)
<i>Palaeosycorax tertiariae</i> (MEUNIER, 1905)	Baltic amber (Eocene)
<i>Hoffeinsodes cubacula</i> WAGNER, 2017	Baltic amber (Eocene)
<i>Hoffeinsodes hoffeinsi</i> WAGNER, 2006	Baltic amber (Eocene)
<i>Hoffeinsodes longicauda</i> WAGNER, 2017	Baltic amber (Eocene)
<i>Hoffeinsodes obtusa</i> WAGNER, 2017	Baltic amber (Eocene)
<i>Hoffeinsodes reducta</i> WAGNER, 2017	Baltic amber (Eocene)
<i>Palaeoglaesum bisulcum</i> WAGNER, 2017	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum carsteni</i> SKIBIŃSKA, KRZEMIŃSKI & ZHANG, 2019*	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum gregi</i> SKIBIŃSKA & KRZEMIŃSKI, 2023***	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum jakubi</i> SKIBIŃSKA, 2023***	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum cracoviae</i> , sp. nov.	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum muelleri</i> WAGNER, 2017	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum myanmari</i> SKIBIŃSKA, 2023***	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum notandum</i> WAGNER, 2017	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum pilosus</i> SKIBIŃSKA, KRZEMIŃSKI & ZHANG, 2021**	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum quadrispiculatum</i> STEBNER, SOLÓRZANO-KRAEMER, IBÁÑEZ-BERNAL & WAGNER, 2015	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum angustum</i> , sp. nov.	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum stebneri</i> SKIBIŃSKA & KRZEMIŃSKI, 2021**	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum teres</i> SKIBIŃSKA & ALBRYCHT, 2021**	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum velteni</i> (WAGNER, 2012)	Burmese amber (Cretaceous, Cenomanian)
<i>Palaeoglaesum wagneri</i> SKIBIŃSKA, KRZEMIŃSKI & ZHANG, 2019*	Burmese amber (Cretaceous, Cenomanian)
<i>Libanonemopalpus grimaldii</i> AZAR, SZWEDO & MAKSOUĐ 2022****	Lebanese amber (Cretaceous, Barremian)

Character states

- 0: Tip of Sc: 0 – reaching costal vein; 1 – atrophied.
- 1: Level of end of Sc: 0 – near midwing; 1 – in proximal region of wing.
- 2: Length of distal section of Sc (distal to connection with sc-r): 0 – several times longer than sc-r (sc-r far from end of Sc); 1 – longer than sc-r; 2 – subequal to sc-r; 3 – shorter than sc-r.
- 3: Level of end of R_1 : 0 – proximal or at same level as end of M_2 ; 1 – distal to end of M_2 .
- 4: Alignment of Rs: 0 – aligned with R_{4+5} ; 1 – aligned with R_{2+3} .
- 5: Length of R_{2+3} : 0 – less than twice length of R_2 ; 1 – at least 2 times as long as R_2 ; 2 – similar or shorter than R_2 .
- 6: Alignment of R_{2+3} : 0 – aligned with R_3 ; 1 – aligned with R_2 .
- 7: Orientation of terminal sections of R_2 and R_3 : 0 – running parallel; 1 – diverging.
- 8: Length of R_2 : 0 – shorter than R_3 ; 1 – similar to R_3 .
- 9: Length of R_{4+5} : 0 – shorter than Rs; 1 – longer than Rs or similar.
- 10: Level of fork of R_{4+5} : 0 – proximal to level of fork of M_{1+2} ; 1 – at same level as fork of M_{1+2} ; 0 – distal to level of this fork of M_{1+2} .
- 11: Length of basal section of R_5 (proximal to connection with r-m): 0 – shorter than r-m; 1 – longer than or similar to r-m.

- 12: Radial end of r-m connected to: 0 – R_{4+5} ; 1 – R_5 .
- 13: Medial end of r-m connected to: 0 – M_{1+2} ; 1 – fork of M_{1+2} ; 2 – M_1 .
- 14: Inclination of r-m: 0 – oblique; 1 – verticalized.
- 15: Level of fork of Mb: 0 – proximal to tip of A_1 ; 1 – at same level as tip of A_1 ; 2 – between tips of A_1 and Cu; 3 – distal to tips of Cu.
- 16: Length of section of M_{1+2} distal to r-m: 0 – shorter than half length of R_{4+5} ; 1 – longer than half length of R_{4+5} , but shorter than R_{4+5} ; 2 – as long as R_{4+5} .
- 17: Alignment of M_{1+2} : 0 – aligned with M_2 ; 1 – aligned with M_1 .
- 18: Orientation of terminal sections of M_2 and M_3 : 0 – running parallel; 1 – divergent.
- 19: Crossvein m-m: 0 – present; 1 – absent.
- 20: Shape of M_4 : 0 – straight; 1 – curved to costal margin.
- 21: Length of basal section of M_4 (proximal to connection with m-cu): 0 – shorter than m-cu; 1 – longer than m-cu.
- 22: Insertion of m-cu: 0 – in M_{3+4} ; 1 – at fork of M_{3+4} ; 2 – in M_4 .
- 23: Shape of Cu: 0 – straight; 1 – only terminal section abruptly curved; 2 – arched.
- 24: Inclination of Cu distal to connection with m-cu: 0 – abruptly bent to anal margin; 1 – straight.
- 25: Level of terminal section of Cu: 0 – proximal to level of fork of Rs; 1 – distal to level of fork of Rs.
- 26: Distance between tips of A_1 and Cu: 0 – similar to distance between Cu and M_4 ; 1 – 0 – shorter than distance between Cu and M_4 ; 2 – longer than distance between Cu and M_4 .
- 27: Base of A_1 : 0 – straight; 1 – kinked.
- 28: End of A_1 : 0 – reaching wing margin; 1 – atrophied.
- 29: Male terminalia: 0 – not inverted; 1 – inverted.
- 30: Length of proctiger: 0 – longer than gonocoxite; 1 – shorter than gonocoxite.
- 31: Shape of groove between cercus lobes: 0 – quadrate, lobes running parallel; 1 – U-shaped, lobes diverging.
- 32: Proportions of epandrium: 0 – longer than wide; 1 – as long as wide.
- 33: Shape of tip of epandrium: 0 – non-differentiated; 1 – dilated.
- 34: Base of epandrium: 0 – non-differentiated; 1 – expanded ventrally.
- 35: Tip of epandrium: 0 – non-branched; 1 – bifid.
- 36: Length of parameres: 0 – developed, but not surpassing aedeagus; 1 – surpassing level of aedeagus; 2 – atrophied, much shorter than aedeagus.
- 37: Tips of parameres: 0 – non-differentiated; 1 – dilated.
- 38: Curvature of aedeagus: 0 – straight; 1 – curved distad.
- 39: Tip of aedeagus: 0 – non-branched; 1 – bifid.
- 40: Orientation of branches of bifid aedeagus: 0 – divergent; 1 – parallel.
- 41: Length of branches of bifid aedeagus: 0 – longer than half of length of aedeagus; 1 – shorter than half of length of aedeagus.
- 42: Hypandrium: 0 – free; 1 – fused with gonocoxite.
- 43: Shape of fused gonocoxite: 0 – angulated; 1 – straight.
- 44: Width of distal region of fused gonocoxite in lateral view: 0 – narrow; 1 – as wide as fused gonocoxite.
- 45: Setae of fused gonocoxite: 0 – on dorsal margin; 1 – concentrated on apex.
- 46: Shape of gonocoxite: 0 – tubular; 1 – with a distal re-entrance on margin.
- 47: Shape of gonocoxite: 0 – not surpassing gonostylus (gonostylus terminal); 1 – gonostylus subterminal, but gonocoxite does not cover entire gonostylus; 2 – gonostylus subterminal, with gonocoxite covering entire gonostylus.
- 48: Length of gonostylus: 0 – shorter than gonocoxite; 1 – similar to or longer than gonocoxite, but shorter than twice length of gonocoxite; 2 – at least 2 times longer than gonocoxite.
- 49: Base of gonostylus: 0 – non-differentiated; 1 – wide.
- 50: Shape of tip of gonostylus: 0 – straight; 1 – bent to base; 2 – curved distad.
- 51: Two lateral projections in gonostylus: 0 – absent; 1 – present.
- 52: Branches of gonostylus: 0 – only one; 1 – presence of a dorsal branch; 2 – presence of a ventral branch.
- 53: Dorsal margin of tip of gonostylus: 0 – smooth; 1 – crested with thorns.

The parsimony analysis with implied weights under different k values resulted in the same single most parsimonious tree, shown in Fig. 5. The most parsimonious tree has a Consistency Index (CI) = 0.38 and a Retention Index (RI) = 0.70. The synapomorphies of each clade are shown in the cladogram (see the Appendix).

Table 2

Data matrix with 39 terminal taxa and 54 characters

	000000000111111111122222222233333333334444444445555
	012345678901234567890123456789012345678901234567890123
<i>Grauvogelia arzvilleriana</i>	0000000000-000200000-0000000????????????????????????
<i>Dacochile browni</i>	013002100021100011000020001000?0000--00--0---00000000
<i>Phlebotomites aphoe</i>	0120-0100--1-00?-001002000?1000?00001000--0---00100000
<i>Alexandria thailandensis</i>	0111020010001002110100010011000000000000--0---00100000
<i>Bruchomyia mineira</i>	11-102001110100201010-111011100000002000--0---00000010
<i>Eutonnoiria edwardsi</i>	11-102001020100-2001002010-110?000002000--0---00102000
<i>Laurenceomyia dampfianus</i>	0111011001201200-101002000-11000000000000--0---00100020
<i>Nemopalpus parvus</i>	011002001110110--101002110-1100000001000--0---00000000
<i>Notofairchildia motacuensis</i>	11-10100000010002001012100-110100000?0????0---00000020
<i>Boreofairchildia belti</i>	?1?001000000100110010-111011100000000000--0---00010110
<i>Boreofairchildia dominicana</i>	0110010000001?0?00?11?1110??00000000??0?--0---00010101
<i>Boreofairchildia henniginus</i>	?1?001000100100310011-1110111????????????????????????
<i>Boreofairchildia scheveni</i>	01?00100000010011001102110110000000000000--0---00010101
<i>Hoffeinsodes adamowiczi</i>	013112111000100000110-101011000000101100--100012000020
<i>Hoffeinsodes bifida</i>	11-102101110111201110021101100000011?00--111011000020
<i>Hoffeinsodes cubicula</i>	????????????????????????????????????0100110??0?--111111000020
<i>Hoffeinsodes hoffeinsi</i>	0131021110011002011100211011000?00101100--100012000020
<i>Hoffeinsodes longicauda</i>	0131021010011012101100211011001?0010??0?--110011000020
<i>Hoffeinsodes obtusa</i>	11-1021111111112-1110021101100000010?00--111011000020
<i>Hoffeinsodes reducta</i>	11-1001011001012211100211011001001101100--111111000020
<i>Libanonemopalpus grimaldii</i>	012001000000100200010-1100110????????????????????????
<i>Palaeoglaesum angustum</i>	0011110110011000200100201011010100000011100---00000000
<i>Palaeoglaesum bisulcum</i>	0031021?100?100??0?10122?1?1010000001?00--0---00100010
<i>Palaeoglaesum carsteni</i>	0011110110001000100100201111010100002011100---00000010
<i>Palaeoglaesum cracoviae</i>	0011110110001002200100201021010?00002011010---00001000
<i>Palaeoglaesum gregi</i>	0011110010001002200100201011010100002011100---00002020
<i>Palaeoglaesum jakubi</i>	001111001000100?0001002210?101??0??02011100---00202020
<i>Palaeoglaesum myanmari</i>	0011011010011002100101221111010000?02011100---00100000
<i>Palaeoglaesum muelleri</i>	001112?11001100000010122111101000000??11100---00001000
<i>Palaeoglaesum notadum</i>	0031021110011000000101221111010000002?11100---00100000
<i>Palaeoglaesum quadrispeculatum</i>	003101001000100220010-121011010100?02011010---00000000
<i>Palaeoglaesum pilosus</i>	0021110110001000000101221111010?00?02011110---00000010
<i>Palaeoglaesum stebneri</i>	001111001001100020010-001011010100000011100---00100000
<i>Palaeoglaesum teres</i>	0011110110001002200101201021010100?02011010---00001010
<i>Palaeoglaesum velteni</i>	003111011000100010010120111101000000??11100---00000000
<i>Palaeoglaesum wagneri</i>	001111111001100?11010??1?1?1010000002011100---00000010
<i>Palaeosycorax inexpectatus</i>	?????00010?0100????1????????00001011??0?--0---10000000
<i>Palaeosycorax molophilinus</i>	011100001000100201110021101100001011??0?--0---10000000
<i>Palaeosycorax tertiare</i>	01110000110010030111002110?100101010100?--0---10000000

V. DISCUSSION

Psychodomorpha is a well-established lineage, documented since the Triassic by the family Grauvogeliidae (KRZEMIŃSKI et al. 1994; BLAGODEROV et al. 2007). AZAR et al. (1999) hypothesised that Psychodidae was as diverse in the Early Cretaceous as it is now. Although an old discussion on the relation between the families of Psychodomorpha still remains open (WAGNER 2017), the close relationship between Tanyderidae and Psychodidae is well established (CRAMPTON 1926; HENNIG 1973; KRZEMIŃSKI and KRZEMIŃSKA 2003; BERTONE et al. 2008; WIEGMANN et al. 2011).

However, the relations within the Bruchomyiinae still remains uncertain. Although classic hypotheses support a close relationship between Bruchomyiinae and Phlebotominae (FAIRCHILD 1952; SATCHELL 1953; HENNIG 1972; AZAR et al. 1999), new studies have highlighted a different scenario. According to a phylogeny of psychodid subfamilies based on molecular data by CURLER and MOULTON (2012), Bruchomyiinae is a sister group of Phlebotominae + Psychodinae. The most recent phylogenetic efforts have been made with molecular data in small lineages (e.g., ESPINDOLA et al. (2012)). However, the positioning of the fossil species remains neglected, although there is a general understanding of the importance of these extinct lineages in the phylogeny of the infraorder (WAGNER & STUCKENBERG 2016).

The most comprehensive phylogeny of Bruchomyiinae is based only on extant species (WAGNER and STUCKENBERG 2016). Their study explored the intrinsic diversity of the genera, and acknowledged the genera *Nemopalpus* and *Notofairchildia* as paraphyletic. Although WAGNER and STUCKENBERG (2016) stated that Baltic amber fossils represent separate phylogenetic lineages, our results show a close relationship between the Baltic amber genera *Hoffensoides* and *Palaeosycorax*. They are combined in one phylogenetic lineage, which could be treated as a sister group to *Nemopalpus*, *Eutonnoiria* and *Bruchomyia*. Both of the analyses show that *Eutonnoiria* is closely related to *Nemopalpus*.

Contrary to WAGNER and STUCKENBERG (2016), the phylogenetic analysis we conducted is based on both fossil and recent species. Our results prove that in phylogenetic analyses the inclusions in fossil resins can be successfully combined with those of recent species, as they provide us with morphological data at almost the same level as contemporary specimens. Their very good state of preservation also allows us to determine the direction of evolution (polarity) of the studied features.

The only phylogeny based on fossil Bruchomyiinae was performed by AZAR et al. (2022). The resulting tree shows *Libanonemopalpus* as a sister group to the remaining Bruchomyiinae, which are shown as an unresolved polytomy. Our results reinforce the positioning of *Libanonemopalpus*. This genus stands out from other members of the subfamily, due to its well-developed piercing mouthparts. According to HENNIG (1972), the reduction of the mouthparts in Bruchomyiinae is a derived character that resulted from a shift in the diet away from hematophagy. *Libanonemopalpus* retains the plesiomorphic ancestral state having haematophagous structures. It is also remarkable that this genus is the oldest lineage of the subfamily, present in Lebanese amber (lower Barremian; MAKSOUD et al. 2021).

The main changes in the taxonomy of the fossil lineages of Bruchomyiinae were introduced by WAGNER (2017), who made a significant contribution to our knowledge of the relationships between the genera *Hoffensoides*, *Palaeosycorax*, *Boreofairchildia* and *Palaeoglaesum*, all described from fossil resins. Our analysis has further reinforced these changes and confirmed a monophyletic and independent status of these genera. We also found a close relation between *Hoffensoides* and *Palaeosycorax*, as was suggested by WAGNER (2017). On the other hand, this author placed in *Palaeoglaesum* the Burmese species previously placed in *Nemopalpus*, while our results show that this is the best option to isolate these different lineages (Fig. 6).

WAGNER and STUCKENBERG (2016) hypothesised that the geological time scale may be used as a benchmark when comparing extant and extinct taxa. However, there is no direct relationship between the age of ambers and the phylogeny. In our analysis, the most supportive evidence for this statement is the position of recent species more basal than those of the extinct genera, as *Palaeoglaesum*.

Somewhat similar conclusions concern the biogeography. The Baltic amber genera are often related to Old World fauna, but recent representatives of Bruchomyiinae (genus *Boreofairchildia*) live in northern South America, Central America, southern North America, the Bahamas and the Caribbean (WAGNER and STUCKENBERG 2016). Moreover, the great morphological diversity in their male terminalia indicates that this lineage was once more widespread and diverse, and that recent taxa represent only a small sample of the bruchomyiine fauna, now restricted to less than 60 species. This indicates the relictual aspect of Bruchomyiinae (AZAR et al. 2022; SKIBIŃSKA et al. 2020; WAGNER and STUCKENBERG 2016).

The study of Bruchomyiinae offers valuable insights into its own history and the evolutionary dynamics within the Psychodomorpha. However, many questions still remain unsolved. As a result, researchers are working diligently to expand our knowledge of fossil Bruchomyiinae. As was stated by AZAR et al. (2022), it is essential to improve our understanding of extinct species, mainly Cretaceous ones, to bridge the existing knowledge gaps. Despite recent progress, the information available on fossil Bruchomyiinae remains somewhat limited, and the appearance of new material is necessary to establish the phylogenetic relationships within this group and its relationship to the other subfamilies of the Psychodidae family.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

APPENDIX

Cladogram underlying the phylogenetic tree.

REFERENCES

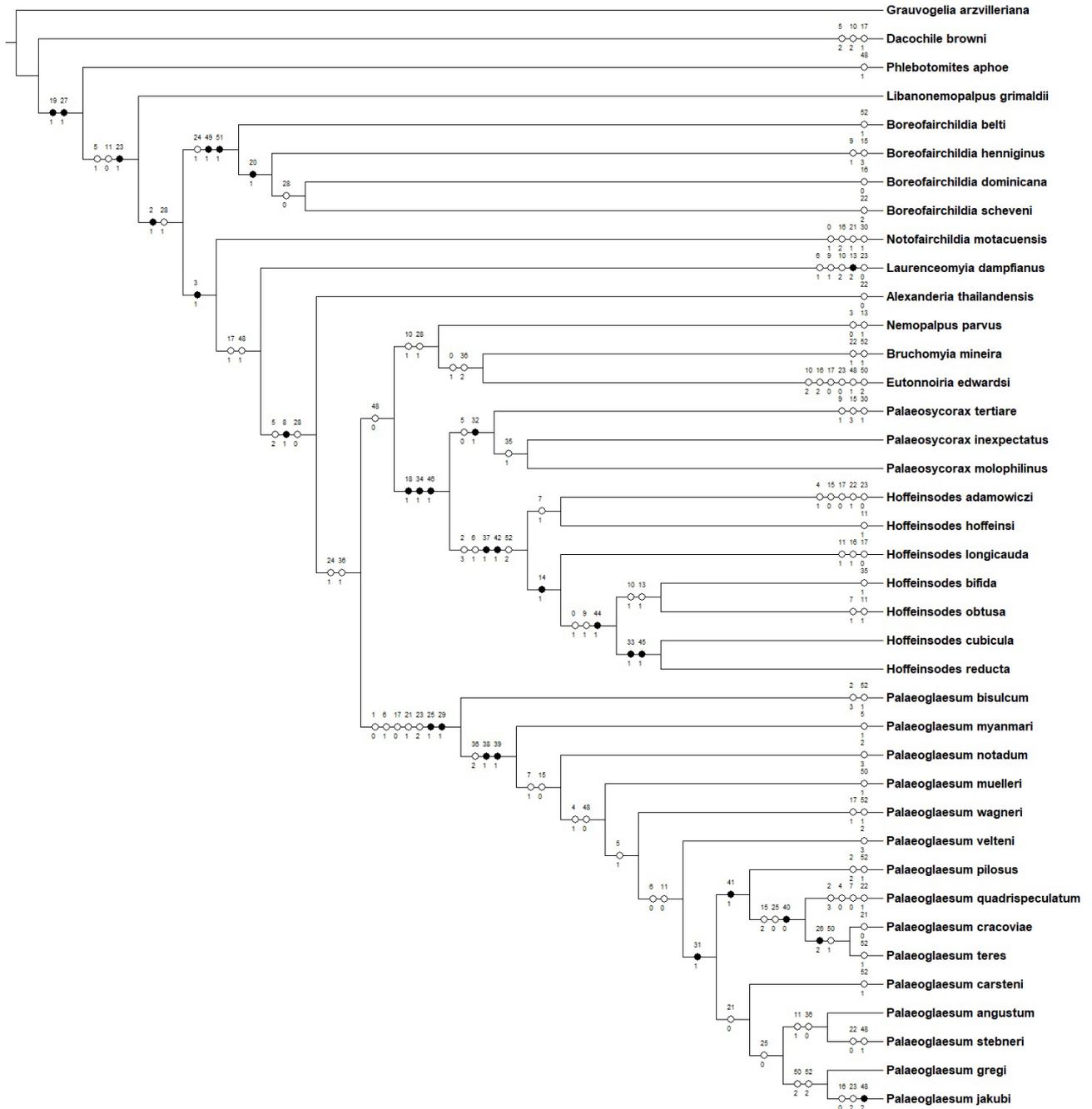
- ALEXANDER C.P. 1920. A new subfamily of Tanyderidae flies (Diptera). *Annals of the Entomological Society of America*, **13**(4): 402-406. <https://doi.org/10.1093/aesa/13.4.402>
- ALEXANDER C.P. 1940. Further observations on the psychodid subfamily Bruchomyiinae (Diptera). *Revista de Entomologia*, **11**: 793-799.
- ANSORGE J. 1994. Tanyderidae and Psychodidae (Insecta: Diptera) from the lower Jurassic of northeastern Germany. *Paläontologische Zeitschrift*, **68**(1-2): 199-210. <https://doi.org/10.1007/BF02989440>
- AZAR D., NEL A., SOLIGNAC M., PAICHELER J.C., BOUCHET F. 1999. New genera and species of psychodoid flies from the Lower Cretaceous amber of Lebanon. *Palaeontology*, **42**(6): 1101-1136. <https://doi.org/10.1111/1475-4983.00112>
- AZAR D., SZWEDO J., MAALOUF M., MAALOUF R., MAKSOUD S. 2022. *Libanonemopalpus grimaldii*, a new genus and species of Bruchomyiinae from Lower Cretaceous Lebanese amber (Diptera: Psychodidae). *Palaeoentomology*, **5**(6): 569-578. <https://doi.org/10.11646/palaeoentomology.5.6.7>
- BERTONE M.A., COURTNEY G.W., WIEGMANN B.M. 2008. Phylogenetics and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. *Systematic Entomology*, **33**: 668-687. <https://doi.org/10.1111/j.1365-3113.2008.00437.x>
- BLAGODEROV V., GRIMALDI D.A., FRASER N.C. 2007. How times flies for flies: diverse Diptera from the Triassic of Virginia and early radiation of the order. *American Museum Novitates*, **3572**: 1-39. [https://doi.org/10.1206/0003-0082\(2007\)509\[1:HTFFFD\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2007)509[1:HTFFFD]2.0.CO;2)
- BRAVO F., BARATA R.A. 2012. A new species of *Bruchomyia* (Diptera: Psychodidae) from caverns in the state of Minas Gerais, Brazil. *Zoologia*, **29**(5): 455-458. <https://doi.org/10.1590/S1984-46702012000500009>
- CRAMPTON G.C. 1926. A phylogenetic study of the thoracic sclerites of the Psychodoid Diptera, with remarks on the interrelationships of the Nematocera. *Entomological News*, **37**(3): 33-39 and 65-70.
- CUMMING J.M., WOOD D.M. 2017. Adult morphology and terminology. [In:] A.H. KIRK-SPRIGGS, B.J. SINCLAIR (eds) Manual of Afrotropical Diptera, Volume 1. Introductory chapters and keys to Diptera families. South African National Biodiversity Institute, Pretoria. Pp: 89-133.
- CURLER G.R., MOULTON J.K. 2012. Phylogeny of psychodid subfamilies (Diptera: Psychodidae) inferred from nuclear DNA sequences with a review of morphological evidence for relationships. *Systematic Entomology*, **37**(3): 603-616. <https://doi.org/10.1111/j.1365-3113.2012.00634.x>
- CURLER G.R., JACOBSON A.J. 2012. New species of Psychodidae (Diptera) from Australasia, with a checklist of the world species of Bruchomyiinae and Sycoracinae. *Zootaxa*, **3552**: 43-65. <https://doi.org/10.11646/zootaxa.3552.1.3>
- EDWARDS F.W. 1921. A note on the subfamily Bruchomyiinae (Diptera Nematocera). *Annals and Magazine of Natural History*, **9**: 437-439.
- ENDERLEIN G. 1936. Klassifikation der Psychodiden (Dipt.). *Deutsche Entomologische Zeitschrift*, **1936**(3-4): 81-112. <https://doi.org/10.1002/mmnd.193619360301>
- ESPINDOLA A., BUERKI S., JACQUIER A., JEŽEK J., ALVAREZ N. 2012. Phylogenetic relationships in the subfamily Psychodinae (Diptera, Psychodidae). *Zoologica Scripta*, **41**(5): 489-498. <https://doi.org/10.1111/j.1463-6409.2012.00544.x>
- EVENHUIS N.L. 1994. Catalogue of the fossil flies of the world (Insecta: Diptera). Backhuys Publishers, Leiden. 660 pp.
- FAIRCHILD G.B. 1952. Notes on *Bruchomyia* and *Nemopalpus* (Diptera, Psychodidae). *Annals of the Entomological Society of America*, **45**(2): 259-280. <https://doi.org/10.1093/aesa/45.2.259>
- GOLOBOFF P.A. 1993. Estimating character weights during tree search. *Cladistics*, **9**(1): 83-91. <https://doi.org/10.1111/j.1096-0031.1993.tb00209.x>

- GOLOBOFF P.A., CATALANO S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, **32**(3): 221-238. <https://doi.org/10.1111/cla.12160>
- HANSON W.J. 1968. The immature stages of the subfamily Phlebotominae in Panama Diptera: Psychodidae. Doctoral Thesis, Faculty of the Graduate School of the University of Kansas 104 pp.
- HENNIG W. 1972. Insektenfossilien aus der unteren Kreide IV. Psychodidae (Phlebotominae), mit einer kritischen Übersicht über das phylogenetische System der Familie und die bisher beschriebenen Fossilien (Diptera). *Stuttgarter Beiträge zur Naturkunde*, **241**:1-69.
- HENNIG W. 1973. 31. Diptera (Zweiflügler). Handbuch der Zoologie, IV. Band: Arthropoda-2. Hälfte: Insecta. Zweite Auflage. 2, Teil: Spezielles (ed. by J.G. Helmke D. Stark and H. Wermuth). Walter de Gruyter, Berlin, 337 pp.
- JEŽEK J., OBOŇA J., PONT F., MAES J.M., MOLLINEDO S. 2018. Two new species of Bruchomyiinae (Diptera, Psychodidae) from the Neotropical Region. *Zootaxa* **4442**(3): 469-478. <https://doi.org/10.11646/zootaxa.4442.3.8>
- KANIA I., WANG B., SZWEDO J. 2015. *Dicranoptycha* Osten-Sacken, 1860 (Diptera, Limoniidae) from the earliest Cenomanian Burmese amber. *Cretaceous Research*, **52**(B): 522-530. <https://doi.org/10.1016/j.cretres.2014.03.002>
- KRZEMIŃSKI W., KRZEMIŃSKA E., PAPIER F. 1994. *Grauvogelia arzvilleriana* sp. n. – the oldest Diptera species (Lower/Middle Triassic of France). *Acta Zoologica Cracoviensia*, **37**(2): 95-99.
- KRZEMIŃSKI W., KRZEMIŃSKA E. 2003. Triassic Diptera: descriptions and phylogenetic relations. *Acta Zoologica Cracoviensia*, **46**(Suppl.): 153-184.
- LEWIS D.J., YOUNG D.G., FAIRCHILD G.B., MINTER D.M. 1977. Proposal for a stable classification of the Phlebotomine sandflies (Diptera: Psychodidae). *Systematic Entomology*, **2**(4): 319-332. <https://doi.org/10.1111/j.1365-3113.1977.tb00381.x>
- LINNAEUS C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Vol. 1: regnum animale. Laurentius Salvius, Stockholm. Pp: 4120.
- MACQUART P.J.M. 1838. Insectes diptères nouveaux ou peu connus. Tome premier. 1re partie. Roret, Paris. Pp: 5-221.
- MAKSOU D., MAALOUF M., MAALOUF R., AZAR D. 2021. Baskinta and Bqaatouta: Two new early Barremian fossiliferous amber outcrops from Central Lebanon. *Palaeoentomology*, **4**(4): 367-373. <https://doi.org/10.11646/palaeoentomology.4.4.12>
- MEUNIER F. 1905. Monographie des Psychodidae de l'Ambre de la Baltique. *Annales Musei Nationalis Hungarici*, **3**: 235-255.
- NEWMAN E. 1834. Attempted division of British insects into natural orders. *The Entomologist's Monthly Magazine*, **2**: 379-431.
- NIXON K.C. 2002. WinClada, version 1.00.08. Published by the author, Ithaca, 734-745.
- POLSEELA R., WAGNER R., KVIFFTE G.M., RULIK B., APIWATHANASORN C. 2018. Revision of Bruchomyiinae (Diptera, Psychodidae) of the Oriental Region, with description of a new genus and species and discussion of putative male/female antagonistic coevolution. *Insect Systematics and Evolution*, **50**(1): 67-82. <https://doi.org/10.1163/1876312X-00002183>
- RIEGEL G.T., KNISKERN V.B. 1963. Two cases of intestinal myiasis in Illinois. *Transactions of the American Microscopical Society*, **84**: 421-422.
- RONDANI C. 1840. Sopra una specie di insetto dittero. Memoria prima per servire alla ditterologia italiana. Donati, Parma. P. 16.
- RONDANI C. 1856. Dipterologiae Italicae Prodrum. Vol. 1. Genera italica ordinis dipterorum ordinatim disposita et distincta et in familias et stirpes aggregata. Tipographia Alexandri Stoschi, Parmae. P. 228. <https://doi.org/10.5962/bhl.title.8160>
- SANTOS C.B., FALQUETO A., BRAVO F. 2013. A new species of *Nemopalpus* Macquart (Diptera, Psychodidae) from Brazil. *Revista Brasileira de Entomologia*, **57**(4): 374-376. <https://doi.org/10.1590/S0085-56262013005000037>
- SANTOS C.B., FALQUETO A., ALEXANDER B. 2009. Description of three new species of *Nemopalpus* (Diptera, Psychodidae, Bruchomyiinae) from Atlantic Forest in southeastern Brazil. *Zootaxa*, **2264**: 58-64. <https://doi.org/10.5281/zenodo.190795>
- SATCHEL G.H. 1953. On the early stages of *Bruchomyia argentina* ALEXANDER (Diptera: Psychodidae). *Proceedings of the Royal Entomological Society of London, Series A*, **28**: 1-12.
- SCHLÜTER T. 1978. Die Schmetterlingsmücken-Gattung *Nemopalpus* (Diptera: Psychodidae) aus dem oligozänen Harz der Dominikanischen Republik. *Entomologia Germanica*, **4**: 242-249.
- SHI G., GRIMALDI D.A., GE H., WANG J., YANG M., LEI W., LI Q., LI X. 2012. Age constraint on Myanmar amber based on U-Pb dating of zircons. *Cretaceous Research*, **37**: 155-163. <https://doi.org/10.1016/j.cretres.2012.03.014>
- SKIBIŃSKA K., KRZEMIŃSKI W., ZHANG Q. 2019. A revised diagnosis of *Palaeoglaesum* WAGNER (Diptera, Psychodidae, Bruchomyiinae) with description of two new species from Cretaceous Myanmar amber. *Historical Biology*, **33**(2): 230-236. <https://doi.org/10.1080/08912963.2019.1607321>
- SKIBIŃSKA K., ZHANG Q., ŠEVČÍK J., KOPEĆ K., KRZEMIŃSKI W. 2023. Description of three new species of *Palaeoglaesum* Wagner (Diptera: Psychodidae, Bruchomyiinae) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, **152**: 105676. <https://doi.org/10.1016/j.cretres.2023.105676>
- SKIBIŃSKA K., ALBRYCHT M., ZHANG Q., GILKA W., ZAKRZEWSKA M., KRZEMIŃSKI W. 2021. Diversity of the Fossil Genus *Palaeoglaesum* WAGNER (Diptera, Psychodidae) in the Upper Cretaceous Amber of Myanmar. *Insects*, **12**(3): 247. <https://doi.org/10.3390/insects12030247>

- SMITH R.D.A., ROSS A.J. 2016. Amberground pholadid bivalve borings and inclusions in Burmese amber: implications for proximity of resin-producing forests to brackish waters, and the age of the amber. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **107**(2-3): 239-247. <https://doi.org/doi:10.1017/S1755691017000287>
- STEBNER F., SOLÓRZANO KRAEMER M.M., IBÁÑEZ-BERNAL S., WAGNER R. 2015a. Moth flies and sand flies (Diptera: Psychodidae) in Cretaceous Burmese amber. *PeerJ*, **3**: e1254. <https://doi.org/10.7717/peerj.1254>
- STEBNER F., SOLÓRZANO KRAEMER M.M., IBÁÑEZ-BERNAL S., WAGNER R. 2015b. Datzinae as a new subfamily name for the unavailable name Protopsychodinae (Diptera: Psychodidae). *PeerJ*, **3**: e1423. <https://doi.org/10.7717/peerj.1423>
- TONNOIR A.L. 1922. Note sur le genre *Nemopalpus* (Psychodidae) et description d'une espèce nouvelle. *Annales de la Société Entomologique de Belgique*, **62**: 125-136.
- TONNOIR A.L. 1939. Psychodidae. Ruwenzori Exped. **1934**(351): 35-80.
- WAGNER R. 2006. Amber Bruchomyiinae – descriptions of already known and new species, and the position of the 'subfamily' within Psychodidae (s. l.) (Diptera). *Studia dipterologica*, **13**: 83-95.
- WAGNER R. 2017. Synopsis of extinct Bruchomyiinae (Diptera, Psychodidae) from Burmese, Baltic and Dominican amber, with descriptions of new genera and species. *Zootaxa*, **4320**(1): 100-120. <https://doi.org/10.11646/zootaxa.4320.1.6>
- WAGNER R., STUCKENBERG B.R. 2012. New fossil and extant species of *Nemopalpus* Macquart (Diptera: Psychodidae, Bruchomyiinae). *African Invertebrates*, **53**(1): 355-367. <https://doi.org/10.5733/afin.053.0119>
- WAGNER R., STUCKENBERG B.R. 2016. Cladistic analysis of Subfamily Bruchomyiinae (Diptera: Psychodidae). *Zootaxa*, **4092**(2): 151. <https://doi.org/10.11646/zootaxa.4092.2.1>
- WIEGMANN B.M., TRAUTWEIN M.D., WINKLER I.S. et al. 2011. Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America*, **108**: 5690-5695. <https://doi.org/10.1073/pnas.1012675108>
- YIN Z., CAI C., HUANG D. 2018. Last major gap in scydmaenine evolution filled (Coleoptera: Staphylinidae). *Cretaceous Research*, **84**: 62-68. <https://doi.org/10.1016/j.cretres.2017.10.026>
- YU T.T., KELLY R., MU L., ROSS A., KENNEDY J., BROLY P., XIA F.Y., ZHANG H.C., WANG B., DILCHER D. 2019. An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences*, **116**(23): 11345-11350. <https://doi.org/10.1073/pnas.1821292116>

APPENDIX

Cladogram underlying the phylogenetic tree (see Fig. 6)



Black circles – synapomorphies, white circles – symplesiomorphies.