

## Article

# Diversity of the Fossil Genus *Palaeoglaesum* Wagner (Diptera, Psychodidae) in the Upper Cretaceous Amber of Myanmar

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**Simple Summary:** Bruchomyiinae is one of seven subfamilies of Psychodidae. In the contemporary fauna, this small, relict subfamily occurs mainly in tropical and sub-tropical regions. Examination of inclusions preserved in the Upper Cretaceous amber of Myanmar (also known as Burmese amber), which is almost 100 mya, shows that this subfamily was abundant during the Cretaceous period. The extinct genus *Palaeoglaesum* is known only from this fossil resin. Moreover, its numerous inclusions and high diversification confirm that the Mesozoic was the stage of the early evolution and radiation of Psychodidae. Here we describe three new species and we provide additional details regarding the morphology of fossil species.

**Abstract:** Cretaceous Myanmar amber is abundant in inclusions belonging to the genus *Palaeoglaesum*. In addition, a significant morphological diversity among representatives of *Palaeoglaesum* can be observed. However, none of its representatives have been found in other fossil materials. Herein three new species: *P. stebneri* sp. nov., Skibińska and Krzemiński *P. teres* sp. nov. Skibińska and Albrycht, and *P. pilosus* sp. nov. Skibińska, Krzemiński and Zhang from Cretaceous Myanmar amber are described and illustrated. The very small size and characters of male hypopygium with aedeagus strongly bent and apically forked are pertinent to diagnosing the genus and species. New materials show that this genus and the whole subfamily Bruchomyiinae were probably more abundant and more diverse than the presently known extant fauna.

**Keywords:** fossil insects; inclusions; Bruchomyiinae; Mesozoic; taxonomy; new species

## 1. Introduction

Bruchomyiinae is one of seven subfamilies of Psychodidae (Diptera). It was originally described as a subfamily of Tanyderidae [1], but Edwards [2] indicated that the group is closely related to some extinct genus of the family Psychodidae. Bruchomyiinae comprises 53 extant species (found on all continents excluding Antarctica) which are restricted to tropical and sub-tropical climates [3]. Adults of this group are reported to be

mostly associated with forest habitats, especially resting in tree hollows or between buttresses. This is supposed to be the main reason why Bruchomyiinae are relatively abundant in the Myanmar amber [4,5]. The genus *Palaeoglaesum* Wagner, 2017 [6] is known only from the Myanmar amber, and to date this is one of the most common genus of this subfamily (personal observation) in this fossil resin. The known fossil fauna consists of seven species, i.e., *P. velteni* [7]; *P. quadrispiculatus* [8]; *P. mulleri* [6]; *P. bisulcum* [6]; *P. notandum* [6]; *P. carsteni* [5] and *P. wagneri* [5]. A general synopsis of *Palaeoglaesum* was provided by Wagner [6] and later diagnosis of the genus has been revised by Skibińska et al. [5]. This extinct group can be distinguished easily from other bruchomyiines by the noticeably smaller size (about 2–2.5 mm) and generally the body is more robustly setose. This character is usually seen particularly well on legs, which possess a fringe of elongate setae and on the head with a median longitudinal strip of setae, recalling in some species the stereotypical Mohawk hairstyle. Also the characteristic shape of male genitalia with aedeagus elongated, arched toward gonopods and with a bifurcated apex is a distinctive feature of the examined genus.

Herein, we provide a description of three new species belonging to the fossil genus *Palaeoglaesum*. This work implies that the subfamily Bruchomyiinae was far more diverse during the Cretaceous period than was previously thought. Moreover, we intend to provide additional details regarding the morphology of fossil species and try to improve our understanding of the evolution of this genus.

## 2. Materials and Methods

Specimens were examined using a Nikon SMZ25 stereomicroscope (located in ISEA PAS, Kraków, Poland) equipped with a Nikon DS-Ri2 digital camera (located in ISEA PAS, Kraków, Poland). Photomicrographs are focus stacks captured using this system and processed using NIS-Elements Imaging Software (located in ISEA PAS, Kraków, Poland). Line drawings were produced by tracing photographs. Interpretation of wing venation follows Byers [9] and Krzemiński and Krzemińska [10]. General morphological terminology follows Cumming and Wood [11]. The collections in which the specimens are deposited are as follows, with abbreviations used throughout the text: the Natural History Museum of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland (ISEA PAS); State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (NIGP).

All specimens examined during this study are representatives of Bruchomyiinae preserved as amber inclusion from the Hukawng Valley in Kachin State, northern Myanmar. Burmese amber was dated by Cruickshank and Ko [12] as middle-late Albian based on the index fossil, but Grimaldi et al. [13] estimated the Cenomanian-Turonian age of this resin based on arthropod inclusions. Shi et al., [14] based on U-Pb dating of zircons from the volcanoclastic matrix of the amber, estimated the age of Burmese amber at  $98.79 \pm 0.62$  Ma (earliest Cenomanian).

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## 3. Results

### 3.1. Systematic Paleontology

- Order Diptera Linnaeus, 1758 [15].
- Family Psychodidae Newman, 1834 [16].
- Subfamily Bruchomyiinae Alexander, 1920 [1].
- Genus *Palaeoglaesum* Wagner, 2017 [6].

Type species: *Nemopalpus quadrispiculatus* Stebner, Solórzano-Kremer, Ibáñez-Bernal and Wagner, 2015: 22, figs. 14 a, b, c, d. Myanmar amber; earliest Cenomanian (Cretaceous).

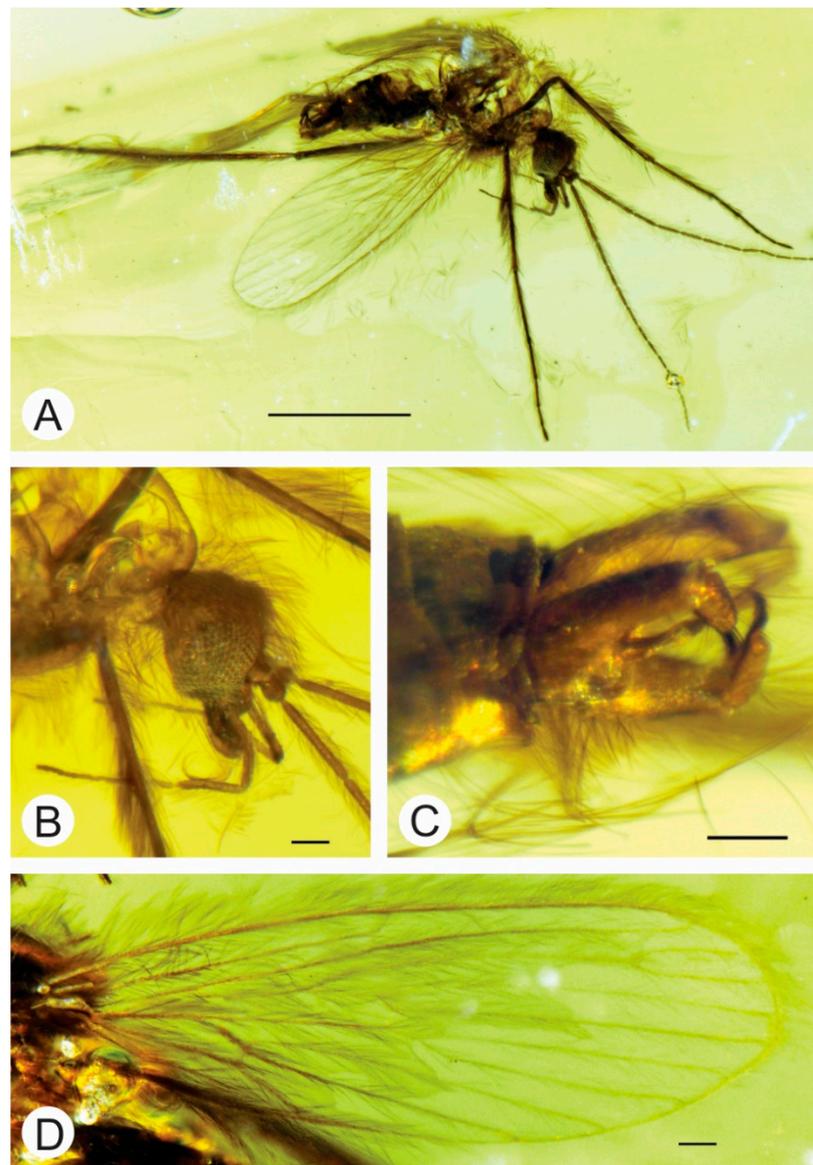
### 3.2. Description of a New Fossil Material

*Palaeoglaesum stebneri* sp. nov. Skibińska and Krzemiński.

LSID urn:lsid:zoobank.org:act:2982B6E0-A9E8-47EF-AE88-6BD476A495CC.

Diagnosis. Male with the following combination of character states: *Wing*: Sc ends almost opposite  $\frac{3}{4}$  of the length of  $R_{4+5}$  and slightly before cross-vein r-m; Rs is  $\frac{1}{3}$  as long as  $R_{4+5}$  and is equal to the length of  $R_2$ ;  $M_1$  slightly more than 4 times longer than  $M_{1+2}$ ; *Male genitalia*: gonostylus single, straight, with a very strong extension of almost  $\frac{2}{3}$  of the basic part; the end part of the gonostylus not forked and strongly tapered, slightly sickle-shaped; aedeagus long, slightly curved with apex bifurcate; parameres strongly curved, only slightly shorter than the aedeagus (Figure 1).

Etymology. The new species is named after Frauke Stebner, a specialist working on fossil Diptera, also on Bruchomyiinae.



**Figure 1.** *Palaeoglaesum stebneri* sp. nov. Photos of the holotype [No. MP/4044]. (A) Whole specimen, scale: 1 mm; (B) head, scale: 0.1 mm; (C) male terminalia, scale: 0.1 mm; (D) wing, scale: 0.1 mm.

Description: Body length: 1.72 mm; wing: length 2.10 mm, width 0.71 mm.

Head: with a crest of elongate setae inserted on vertex and frons; cervical sclerites elongate, longer than width of eyes in lateral view; antennae with elongate-cylindrical flagellomeres decreasing in length (length in mm: 1/0.27; 2/0.18), each constricted at base and apex, covered with dense setae, shorter than those on other body parts, scapus 0.04 mm long, pedicel 0.07 mm long; labellum elongated; palps elongate, five-segmented (length in mm: 2/0.14; 3/0.12; 4/0.16; 5/0.36), basal segment inconspicuous (not possible to measure), ultimate segment strongly elongated, slightly longer than two previous ones combined (Figure 1B).

Thorax: wing is clearly visible; Sc ends almost opposite  $\frac{3}{4}$  of length of  $R_{4+5}$  and slightly before cross-vein r-m;  $R_s$   $\frac{1}{3}$  as long as  $R_{4+5}$  and is equal to e length of  $R_2$ ;  $R_{2+3}$  long, about 3 times longer than  $R_2$ ; cross-vein r-m 3 times shorter than  $M_{1+2}$ ;  $M_1$  slightly more than 4 times longer than  $M_{1+2}$ ;  $M_3$  slightly more than 8 times longer than  $M_{3+4}$ ; cross-vein m-m absent; cross-vein m-cu long, slightly longer than length of cross-vein r-m and located just before fork of  $M_{3+4}$  into  $M_3$  and  $M_4$ ; anal lobe reduced (Figure 1D).

Legs with fringe of setae, most conspicuous at the joint between tibia and tarsi.

Abdomen: in general, typical of Bruchomyiinae; male genitalia elongate, more than three times longer than wide; gonocoxites about 0.18 mm long separate from each other at the base, with translucent membrane in between; gonostylus about 0.13 mm long, in almost  $\frac{2}{3}$  of basic length strongly extended, the end part of the gonostylus strongly narrowed and slightly sickle-shaped; aedeagus long, slightly curved, with apex bifurcate; parameres strongly curved, only slightly shorter than aedeagus (Figure 1A,C).

Material examined. Holotype male, No. MP/4044 deposited in the collection of the ISEA PAS. Myanmar amber, earliest Cenomanian (about 99 Ma).

Additional materials. MP/3704 (male; syninclusions: Araneae and Diptera), MP/3722 (male), MP/4044 (male), MP/4045 (male), MP/4046 (male), MP/4047 (male) MP/4066 (male) all deposited in the ISEA PAS; NIGP 174740 (two males), NIGP 174741 (one male) deposited in the NIGP.

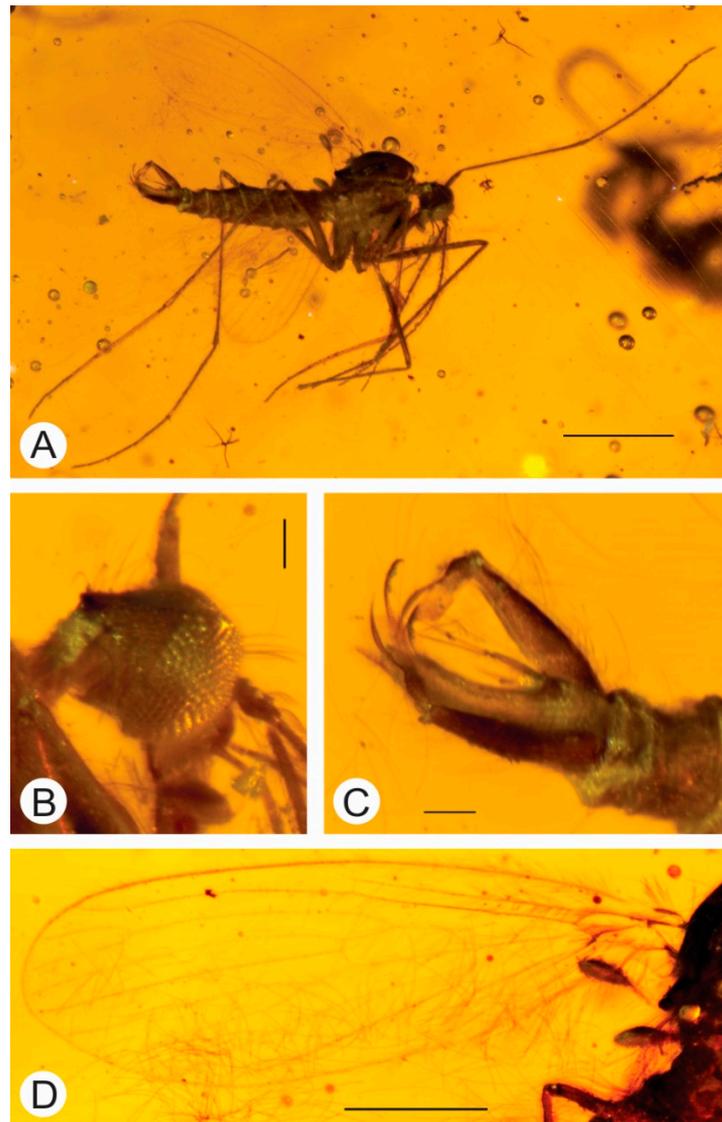
Female unknown.

*Palaeoglaesum teres* sp. nov. Skibińska and Albrycht.

LSID urn:lsid:zoobank.org:act:C5BC6C53-721E-4DCC-BA99-65B38FB5D1E3.

Diagnosis. Male with the following combination of character states: *Wing*: Sc ends just behind the fork of  $R_{4+5}$  into  $R_4$  and  $R_5$  and almost opposite cross-vein r-m;  $R_s$  is twice as long as  $R_{4+5}$  and is slightly shorter than the length of  $R_2$ ;  $M_1$  slightly more than 5 times longer than  $M_{1+2}$ ; *Male genitalia*: small, gonostylus forked, strongly expanded at the basal part; upper part of gonostylus narrow, slightly sickle-shaped, lower part clearly extended at  $\frac{2}{3}$  of its length, strongly tapered and curved at the end; aedeagus strongly curved and bifurcate in apical half; parameres short, strongly sickle-shaped, reaching about half of the aedeagus length (Figure 2).

Etymology. The new species is named after the first king of the Odryian kingdom of Thrace, known mainly for his military skills.



**Figure 2.** *Palaeoglaesum teres* sp. nov. Photos of the holotype [No. MP/3677]. (A) Whole specimen, scale: 1 mm; (B) head, scale: 0.1 mm; (C) male terminalia, scale: 0.1 mm; (D) wing, scale: 0.5 mm.

**Description:** Specimen is well preserved. Body length: 2.2 mm; Wing length 1.9 mm, width 0.73 mm covered with sparse, long setae.

**Head:** with crest of elongate setae inserted on vertex and frons; antennae (boundaries between segments difficult to observe due to elongate setae) with narrow, elongate-cylindrical flagellomeres; first flagellomere about  $\frac{1}{3}$  longer than the next one and subsequent segments progressively shorter; palps elongate (not possible to measure), narrow, with four segments, the last segment is more than half as long as the penultimate one (Figure 2A,B).

**Thorax:** wing venation clearly visible; Sc ends just behind the fork of  $R_{4+5}$  into  $R_4$  and  $R_5$  and almost opposite cross-vein r-m;  $R_s$  twice as long as  $R_{4+5}$  and slightly shorter than length of  $R_2$ ;  $R_{2+3}$  about  $2\frac{1}{2}$  times longer than  $R_2$ ; cross-vein r-m about 2 times shorter than  $M_{1+2}$ ;  $M_1$  slightly more than 5 times longer than  $M_{1+2}$ ;  $M_3$  slightly more than 11 times longer than  $M_{3+4}$ ; cross-vein m-m absent; cross-vein m-cu about half the length of cross-vein r-m and located about its length behind fork of  $M_{3+4}$  into  $M_3$  and  $M_4$ ; anal lobe reduced (Figure 2D).

**Male genitalia:** gonocoxite about 0.32 mm long; gonostylus about 0.22 mm long, forked, strongly expanded at basal part; upper part of gonostylus narrow, slightly sickle-shaped bent, lower part clearly extended at  $\frac{2}{3}$  of its length and strongly tapered and bent

at the end; aedeagus strongly bent and bifurcate in apical half; short parameres, strongly sickle-shaped bent, reaching about half of aedeagus length (Figure 2C and Figure 5B).

**Material examined.** Holotype male, No. MP/3677 deposited in the collection of the ISEA PAS. Myanmar amber, earliest Cenomanian (about 99 Ma). Syninclusions: one Atelestidae, two Hymenoptera, one Brachycera, two Chironomidae, one Psocoptera, one Araneae, one Blattodea.

Female unknown.

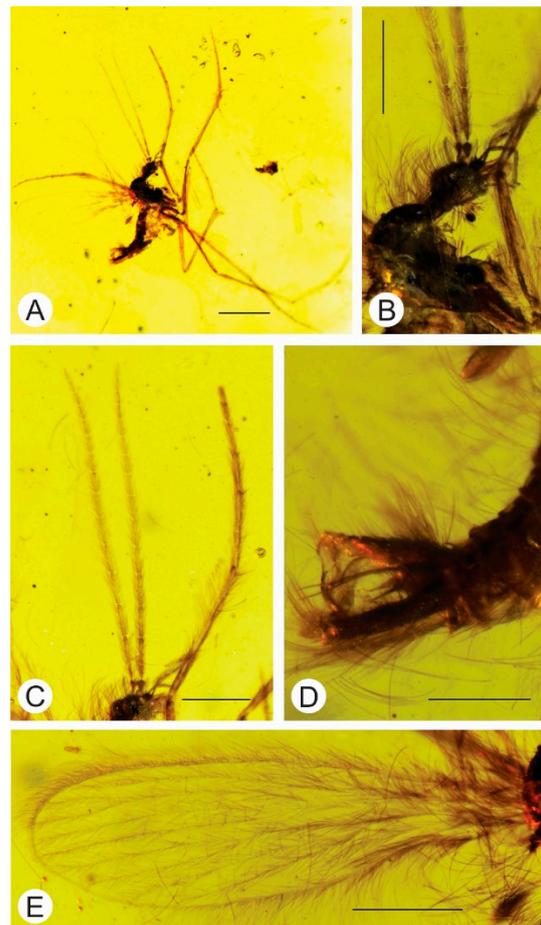
**Remarks.** This species is described based on a single specimen, which suggests that its presence in the fauna was scarce when Myanmar amber was forming. *Palaeoglaesum teres* sp. nov. is slightly similar to *P. wagneri* [5], however, it clearly differs in gonocoxite structure, sickle-like parameres, and the shape of the aedeagus, which is forked for almost half of its length.

*Palaeoglaesum pilosus* sp. nov. Skibińska, Krzemiński and Zhang.

LSID urn:lsid:zoobank.org:act:5DA7219F-01B4-490D-AD17-B0041D02A717.

**Diagnosis.** Male with the following combination of character states: *Wing*: Sc ends almost opposite  $\frac{1}{4}$  of the length of  $R_{4+5}$  and clearly before cross-vein r-m;  $R_s$  is  $\frac{1}{3}$  as long as  $R_{4+5}$  and is slightly longer than the length of  $R_2$ ;  $M_1$  slightly more than 9 times longer than  $M_{1+2}$ . *Male genitalia*: gonostylus with a large appendix on the external edge, strongly expanded in a mid-length and tapered at the end; aedeagus strongly curved and bifurcated at about  $\frac{1}{3}$  of its length; short, sickle-shaped parameres, reach about  $\frac{1}{3}$  of aedeagus length (Figure 3).

**Etymology.** The specific epithet is in reference to the characteristic hairiness of the body which is typical for the whole genus.



**Figure 3.** *Palaeoglaesum pilosus* sp. nov. Photos of the holotype [NIGP 174742]. (A) Whole specimen, scale: 1 mm; (B) head, scale: 0.5 mm; (C) antennae, scale: 0.5 mm; (D) male terminalia, scale: 0.5 mm; (E) wing, scale: 0.5 mm.

Description. Head, thorax, and legs covered with long and dense setae. Body length about 1.83 mm; wing length about 2.18 mm; wing width about 0.7 mm (Figure 3).

Head: with crest of elongate setae inserted on vertex and frons; cervical sclerites elongate, longer than width of eyes in lateral view; antennae with elongated-cylindrical flagellomeres decreasing in length (length in mm: 1/0.31; 2/0.23) each constricted at base and apex, covered with dense setae, shorter than those on other parts of body, scapus 0.05 mm long, pedicel 0.08 mm long; labellum elongated; palps elongate, with four segments (not possible to measure) (Figure 3A,B).

Thorax: wing venation clearly visible; Sc ends almost opposite  $\frac{1}{4}$  of the length of  $R_{4+5}$  and clearly before cross-vein r-m; Rs is  $\frac{1}{3}$  as long as  $R_{4+5}$  and is slightly longer than the length of  $R_2$ ;  $R_{2+3}$  about  $2\frac{3}{4}$  times longer than  $R_2$ ; cross-vein r-m is about the same length as  $M_{1+2}$ ;  $M_1$  slightly more than 9 times longer than  $M_{1+2}$ ;  $M_3$  almost 12 times longer than  $M_{3+4}$ ; cross-vein m-m absent; cross-vein m-cu short, twice as short as the length of cross-vein r-m and is located slightly further than its length behind the fork of  $M_{3+4}$  into  $M_3$  and  $M_4$ ; anal lobe reduced (Figures 3E and 4C).

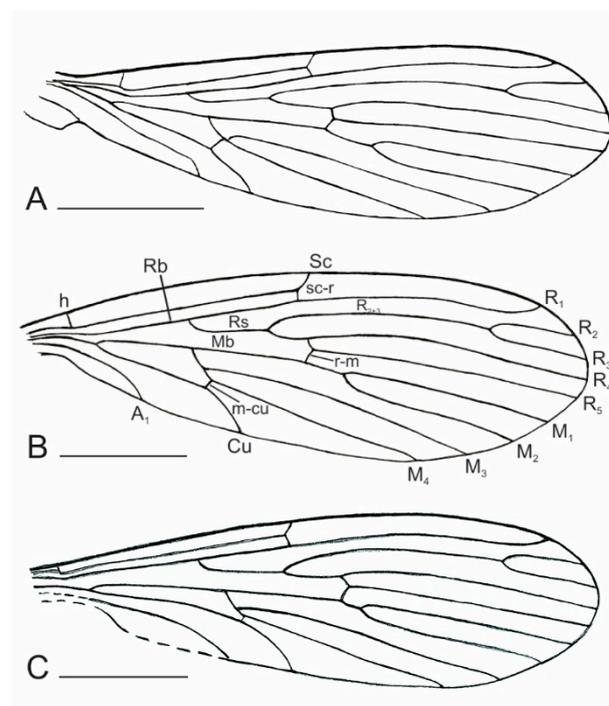
Legs: covered with fringe of setae, most conspicuous at the joint between tibia and tarsi.

Male genitalia: gonocoxite wide at a base, about 0.27 mm long; gonostylus about 0.20 mm long with a large appendix on the external edge, strongly extended at mid-length and visibly tapering to a point; aedeagus strongly curved and bifurcated at about  $\frac{1}{3}$  of its length; short, sickle-shaped parameres, reach about  $\frac{1}{3}$  of the aedeagus length (Figures 3C and 5C).

Material examined. Holotype male, NIGP 174742 deposited in the collection of NIGP. Myanmar amber, earliest Cenomanian (about 99 Ma).

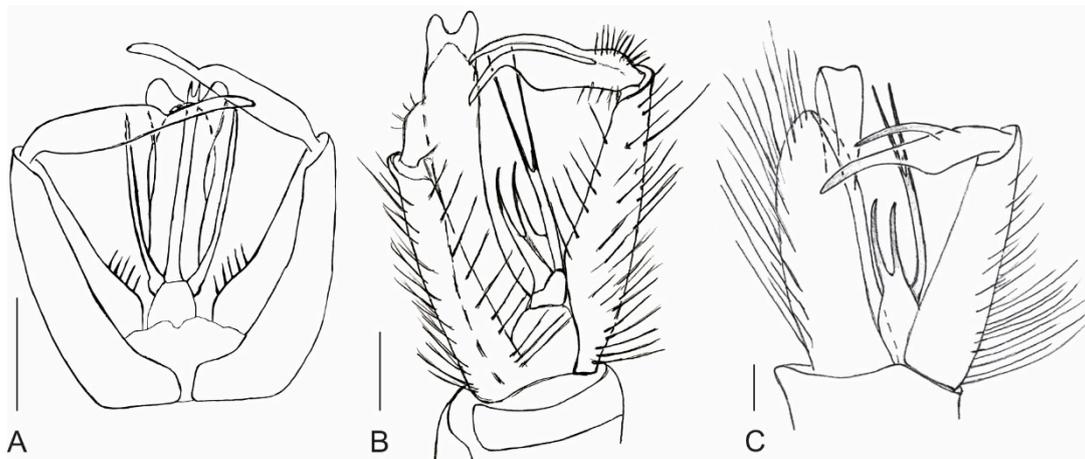
Additional materials. NIGP 174743 male, NIGP 174744 male deposited in the collection of NIGP, and MP/4047 male deposited in the collection of ISEA PAS.

Female unknown.



**Figure 4.** Line drawings of wing venation of (A) *P. stebneri* sp. nov.; (B) *P. teres* sp. nov.; (C) *P. pilosus* sp. nov. Scales: 0.5 mm. Abbreviations: A<sub>1</sub> = first anal vein; Cu = cubital vein; M<sub>1</sub> = first branch of media; M<sub>2</sub> = second branch of media; M<sub>3</sub> = third branch of media; M<sub>4</sub> = fourth branch of media; R<sub>1</sub> = anterior branch of radius; R<sub>2</sub> = upper branch of second branch of radius; R<sub>3</sub> = lower branch of

second branch of radius;  $R_4$  = upper branch of third branch of radius;  $R_5$  = lower branch of third branch of radius; Sc = subcostal vein.



**Figure 5.** Line drawings of male genitalia of (A) *P. stebneri* sp. nov.; (B) *P. teres* sp. nov.; (C) *P. pilosus* sp. nov., scales: 0.1 mm.

#### 4. Discussion

Currently, Myanmar amber is of great interest among researchers. Its popularity is the effect of a huge variety of inclusions, their relatively high repeatability, and good state of preservation. Additionally, we find there both representatives of extinct evolutionary lines as well as the first evidence of the presence of contemporary Diptera groups. The first fossil Psychodidae were reported from the early Jurassic [17], and therefore they constitute one of the oldest clades of Diptera. Representatives of this family are found in subsequent geological periods, including all types of fossil resin, but their diversity and repeatability is considered to be the most numerous in Cretaceous Myanmar amber. In this fossil resin, significant differences between species and great diversity can also be observed within this ancient family, indicating its rapid evolutionary development during the Cretaceous period. Only from this fossil resin representatives of the extinct subfamily Datziniinae [8] or the unique fossil Horaiellinae [18] were reported. Unfortunately, despite the huge number of inclusions available for research, so far no inclusions of larvae or pupae of genus *Palaeoglaesum* have been found and the larval habitat remains unknown, and it requires more materials to solve this issue. However, it seems that in the areas of amber resin production there were relatively few typically aquatic environments, but there could have been more environments with shallow, periodic water reservoirs and places with damp soil. Description of Bruchomyiinae larva which lives in forest litter, caves and moist, decomposed organic material [19] suggesting that *Palaeoglaesum* does not need water reservoirs for its growth and that dark and damp places were enough.

Our study confirms that *Palaeoglaesum* is the most species-rich genus of Bruchomyiinae found in the Myanmar amber. Currently, including the three new species described herein, a total of 10 are now recorded. Interestingly, such a well-represented and so highly diversified genus is known only from Myanmar amber and has not been described so far from other Cretaceous fossil resins such as Spanish or French amber. Consecutive described species indicate that contemporary representatives of the subfamily Bruchomyiinae should be treated as a relict group, which was far more widespread and diverse through the Mesozoic. However, it is highly plausible that its abundance was already significantly reduced in the Eocene, as only 13 species have been described from Baltic amber [20]. Moreover, it seems that this subfamily represented mainly by the genus *Palaeoglaesum* was dominant during this period (personal observation). However, it is interesting that subfamilies which are very common in contemporary fauna are relatively scarce (Trichomyiinae) or not present (Psychodinae) in Myanmar amber [21].

## 5. Conclusions

New fossil materials show that during the Cretaceous period Bruchomyiinae live through very rapid radiation which resulted in the creation of many new species, moreover it seems that in this subfamily the genus *Palaeoglaesum* was one of the most widespread genera and could be easily distinguished by its small size and specific male genitalia with a sickle-bent, bifurcated aedeagus.

Up until now, there have been no descriptions of larvae or pupas of this genus so the larval habitat of *Palaeoglaesum* remains unknown. However, the remarkably rich *Palaeoglaesum* inclusions in Myanmar amber may suggest that an environment with shallow, periodic water reservoirs and many places with damp soil were ideal for the development of these flies.

**Author Contributions:** Conceptualization, K.S. and W.K.; methodology, K.S. and W.K.; validation, K.S., W.K., and Q.Z.; investigation, K.S., W.K., and M.A.; resources, K.S. and W.K.; writing—original draft preparation, K.S., W.K., M.A., W.G., M.Z., and Q.Z.; writing—review and editing, K.S., W.K., M.A., W.G., M.Z., and Q.Z.; visualization K.S., W.K., and M.A.; supervision, K.S. and W.K.; project administration, K.S. and W.K.; funding acquisition, W.K., K.S., M.A., and Q.Z. All authors have read and agreed to the published version of the manuscript.

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**Conflicts of Interest:** The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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