

# Eco-morphological diversity of larvae of soldier flies and their closer relatives in deep time

Viktor Baranov<sup>1</sup>, Yinan Wang<sup>2</sup>, Rok Gašparič<sup>3</sup>, Sonja Wedmann<sup>4</sup>, Joachim T. Haug<sup>1,5</sup>

Corresponding Author:

Viktor Baranov<sup>1</sup>

1 Biology II, Ludwig-Maximilians-Universität München, Munich, Bayern,

Germany.

2 Association of Applied Paleontological Sciences, Logan, Utah, United States.

3 Department of Geology, University of Ljubljana, Ljubljana, Slovenia.

4 Department of Palaeoanthropology and Messel Research, Senckenberg Nature Research Society, Frankfurt am Main, Germany, Hesse, Germany

5 Geobiocenter, Ludwig-Maximilians-Universität München, Munich, Bayern,

Germany.

Email address: baranow@biologie.uni-muenchen.de

## **Abstract**

Stratiomyomorpha (soldier flies and allies) is an ingroup of Diptera, with a fossil record stretching back to the Early Cretaceous (the Barremian, about 125 MYA). Stratiomyomorpha includes at least 3000 species in the modern fauna, with many species being crucial for ecosystem functions, especially as saprophages. Larvae of many stratiomyomorphans are especially important as scavengers and saproxyls in modern ecosystems. Yet, fossil larvae of the group are incredibly scarce. Here we present 23 new records of fossil stratiomyomorphan larvae, representing **six** discrete morphotypes. Specimens originate from Cretaceous amber from Myanmar, Eocene Baltic amber, Miocene Dominican amber, and compression fossils from the

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted: Department of Biology II, LMU Munich, Großhaderner Str. 2, 82152, Martinsried-Planegg, Germany. 1 Biology II,

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Eocene of Messel (Germany) and the Miocene of Slovenia. We discuss the implications of these new records for our understanding of stratiomyomorphan ecomorphology in deep time as well as their palaeoecology.

## Introduction

Stratiomyomorpha is a group of flies (Diptera), which includes more than 3000 species of soldier flies and allies in the modern-day fauna (Pape, Blagoderov, and Mostovski 2011). The major ingroups of Stratiomyomorpha include 1) Stratiomyidae, the group of true soldier flies, 2) Xylomyidae, the group of wood soldier flies, and 3) Pantophthalmidae, the group of giant timber flies (Marshall 2012). The group Stratiomyomorpha has a fossil record reaching back about 125 million years into the past, to the Barremian (Lower Cretaceous; Whalley and Jarzembowski 1985; Mostovski 1998). A now-extinct group of flies with long proboscides (Zhangosolvidae) from the Cretaceous has also been interpreted as an ingroup of Stratiomyomorpha (Peñalver et al., 2015).

Representatives of Stratiomyomorpha are widespread in modern ecosystems and diverse in their biology (Woodley, 2001; Marshall, 2012). Larvae of different ingroups of Stratiomyomorpha vary in their habitat preferences. Fully aquatic larvae are known in Stratiomyinae, Rhabdiocerinae, etc. (ingroups of Stratiomyidae); other larvae develop in the terrestrial habitats as in the groups Pachygastrinae, Clitellariinae, Sargiinae or Hermetiinae (ingroups of Stratiomyidae), and Xylomyidae, while larvae of timber flies (Pantophthalmidae) are saproxylic, burrowing in living wood (James 1981, Rozkošný, 1981, 1982, Pujol-Luz, 2014). Xylomyidae is a small group of flies with predacious or saprophagous larvae living under tree bark (James 1981). Pantophthalmidae, the group of timber flies, including one of the largest extant representatives of Diptera, with larvae burrowing in living wood (Rapp, 2007, 2011).

Representatives of Stratiomyomorpha are carrying vital ecosystem functions in their respective habitats: 1) the larvae often act as essential saprophages, involved in the cycling of organic matter, and 2) adults are essential pollinators (Hauser, Woodley, and Fachin 2017).

One species of soldier flies, namely *Hermetia illucens* (Linnaeus, 1758), with its fast-growing scavenger-type larvae, is considered as an important source of protein for feeding cattle in industrial agriculture or for production of human food (Hauser, Woodley, and Fachin 2017; Lessard et al. 2019). Many merolimnic species of Stratiomyomorpha, i.e., those with aquatic larvae, are important algal mat grazers, involved in carbon cycling (Mángano, Buatois, and Claps 1996).

Ichnofossils attributed to larvae of Stratiomyomorpha are quite common in the fossil record (Mángano, Buatois, and Claps 1996; Pickerill, Han, and Jiang 1998), while body fossils of this group have been extremely rare (Evenhuis 1994). So far, only five deposits are yielding any of them:

1) Whalley & Jarzembowski (1985) reported four stratiomyomorphan larvae, differentiated into two morphotypes, from the Early Cretaceous Montsech (Lerida, Spain, 125.45 to 122.46 Ma) lithographic limestone of Spain.

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

2) Two morphotypes of larvae from Myanmar amber (~100 MYA) were reported by Liu et al. (2019).

3) Kühbänder & Schleich (1994) reported a stratiomyomorph larva, interpreted as a larva of the group *Odontomyia*, from the Miocene Randecker Maar in Germany (~17 MYA). Numerous additional specimens were recorded later from the same deposit (Rasser et al., 2013).

4) Karl & Bellstedt (1989) reported a single body fossil of a larva of the group Stratiomyidae from the Holocene of Eastern Germany (>1 MYA).

5) Sixteen fossil larvae of Stratiomyidae from the late Eocene of the Isle of Wight ( $129.4 \pm 1.5$  MYA) are present in the collection of the Natural History Museum London (U.K.). They can be interpreted as aquatic forms of the group Stratiomyini and have been tentatively suggested to be representatives of the species *Odontomyia brodiei* (Cockerell, 1915), which is known from fossils of adults from the same deposit (Krzeminski et al. 2019).

Larval forms are crucial for the success and diversification of any ingroup of Holometabola, due to the ecological niche separation of the life stages (Grimaldi and Engel 2005). This applies to the super-diverse lineages of beetles (Coleoptera), wasps (Hymenoptera), butterflies (Lepidoptera), and flies (Diptera), but also the less species-rich groups. The severe lack of fossil larvae of Stratiomyomorpha is hampering progress in our understanding of the evolution of the group. Here we report new records of larvae of Stratiomyomorpha based on new fossil specimens. We furthermore discuss the ecological roles of the extinct larval forms based on morphometric comparison of modern and fossil forms.

## Materials & Methods

### Material

Twenty-three specimens of fossil larvae are in the focus of this study. Twenty of them are preserved in amber, and three are preserved as compression fossils. These larvae are representing six morphotypes: two from Myanmar amber, one from Baltic amber, one from Dominican amber, one from the Činžat shale of Slovenia, and the last one from the Messel lake deposits. Most of the specimens in amber originated from Myanmar ("Burmese amber"), and most represent a single morphotype ("morphotype 1"). Working with Burmese amber requires special ethical consideration for the details, to see the ongoing discussion (Haug et al., 2020). All these specimens were purchased on ebay.com from different sellers and are now deposited at the collection of the Palaeo-Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany (PED) (PED -0152, PED-0349, PED-0362, PED-0031, PED-0041, PED-0243, PED-0113, PED-0025).

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

**Commented [VB1]:** Haug, J.T., Azar, D., Ross, A. et al. Comment on the letter of the Society of Vertebrate Paleontology (SVP) dated April 21, 2020 regarding "Fossils from conflict zones and reproducibility of fossil-based scientific data": Myanmar amber. PalZ(2020). <https://doi-org.emedien.uni-muenchen.de/10.1007/s12542-020-00524-9>

Deleted:

A second morphotype (morphotype 2) also preserved in amber from Myanmar is represented by five larval specimens, preserved in a single piece of amber (accession number NHMLA-LACM ENT 366281). This specimen is deposited in the collection of the Los Angeles County Museum of Natural History, Los Angeles, California, USA (LACM).

Specimen PED-0462, representing morphotype 3, was commercially acquired by Y.W., originated from the Dominican Republic, and is now deposited in the collection of the Palaeo-Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany PED research collections (PED).

R.G. collected specimen PED-0463, representing morphotype 4 at the locality, Činžat, situated in the Ribnica-Selnica Graben, northern Slovenia: the specimen is now deposited at the collection of the Palaeo-Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany (PED).

Specimen PED-0464, representing morphotype 5, was obtained commercially from Mr. Jonas Damzen (<http://www.amberinclusions.eu>) and stemmed from Yantarnyj, Kaliningrad district (formerly Palmnicken, Königsberg), it is now deposited in the collection of the Palaeo-Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany (PED).

Finally, two compression fossils originated from the Messel pit fossil site in Germany, representing morphotype 6, are deposited under coll-no. SF-MeI 4666 in the collection of the Forschungsinstitut und Naturmuseum Senckenberg (S.F.), Frankfurt-am-Main, Germany.

For comparative purposes, we used extant larval representatives of Stratiomyidae from the collection of the Zoological State Collection, Munich (Zoologische Staatssammlung München, ZSM), in particular larvae of *Pachygaster atra* (Panzer, 1798), *Oxycera nigricornis* Olivier, 1811, as well as *Odontomyia* sp. The latter is deposited in the collection of the Palaeo-Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany (PED-0465). For a full list of materials, please see Table 1.

**Terminology:** The morphological terminology mostly follows Rozkošný (1981, 1982) and Sinclair (1992) for the head capsule morphology. Yet, to enhance the understanding of non-experts, we amended some of the special morphological terms with more general terms. As Insecta is an accepted ingroup of Crustacea s.l. "crustacean"-names are given in brackets where necessary to provide more comprehensive frame correspondence. It is important to note that many structures cannot be discerned externally in the Diptera larvae, i.e., it is impossible to see any tergite boundaries in the head capsule of the postembryonic larvae. Nevertheless, it is well possible to reconstruct the sequence of the segments in the head capsule, using the arrangement of the appendages (Baranov et al., 2019).

#### Database use

Data on the fossil record of the group Stratiomyomorpha were downloaded from the Paleobiology Database on 09 November 2019, using the group name "Stratiomyomorpha" without any other filtering parameters.

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

## Imaging methods

Amber specimens were imaged using a Keyence VHX-6000 Digital microscope, with ring-light type illumination and/or cross-polarized, coaxial illumination. All images were recorded as composite images to counteract the limitations of depth of the focus. Models were assembled using stitching and panorama functions to overcome the weakness of the field of view under higher magnifications. Each image detail was recorded by a stack of images of shifting focus to overcome the limitation of the depth of field (Haug, Haug, and Ehrlich 2008; Haug et al. 2011; Haug, Müller, and Sombke 2013). Fusion into sharp images and panorama stitching was performed with the built-in software, e.g., in Baranov, Schädel, and Haug (2019). We also employed the built-in HDR function of the digital microscope; therefore, every single frame is a composite from several images taken under different exposure times (cf. Haug et al. 2013). Additionally, some specimens were imaged using a Keyence BZ-9000 fluorescence microscope with either 2×, 4×, 10× or 20× objectives. Observations were conducted at an emitted wavelength of 532 nm since it was the most compatible with the fluorescence capacities of the fossil specimens (Haug et al. 2011). Also, here we recorded stacks of images which then were digitally fused to single in-focus images using CombineZP (GNU). Compression fossils from Messel were photographed with a Leica MZ12.5 stereomicroscope with an attached Nikon D300 camera.

The cuticle fossil, specimen PED-0463 ("morphotype 4"), was additionally imaged using a scanning electron microscopy (SEM). Scanning was performed using a Carl Zeiss Leo 1430VP scanning electron microscope in the Zoologische Staatssammlung München (Germany). Scanning was performed with the beam current 80 μA, filament electric current 2500 A, and electrical potential 10-20 kV. Scanning was performed in a low vacuum (<2e-005 mbar).

## Morphometry and outline analysis

The maximum dorsal head capsule length and width of some larvae were measured from the tip of the labrum to the outer edge of the head capsule. Actual measurements were done from the photos, using ImageJ, a public domain (Schindelin et al. 2012).

As a proxy for the overall shape diversity, we compared the outlines of the larvae in the dorsoventral aspect. To do so, we have analyzed the shapes, more precisely sketches of all specimens, and extant comparative specimens with Fourier Elliptical Transformation using R package Momocs (Bonhomme et al. 2014) and compared morphospace occupancy.

For the outline analysis, we used black-and-white .jpg files, containing the outlines of all available fossil stratiomyomorph larvae as well as all existing stratiomyomorph larvae for which we were able to obtain a full-body image in the dorsoventral aspect from the literature. Only specimens with a relatively straight body were included, as any examples imaged in curled or bent position will heavily bias the morphospace. Full-body images of the larvae were obtained from numerous published sources (Schremmer 1951; Hennig 1952; James 1965; McFadden 1967; Bull 1976; Tuskey 1976; James 1981; Schremmer 1986; Beuk 1990; Rozkošný 1997;

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Rozkošný and Kovac 1998; Pujol-Luz and Xerez 1999; Stubbs and Darke 2001; Stuke 2003; Pujol-Luz, Xerez and Viana 2004; de Xerez and Garcia 2008; Bucánková, Kovac, and Rozkošný 2009; Marques and de Xerez 2009; Marshall 2012; Pujol-Luz and Pujol-Luz 2014a & b; Pujol-Luz, Lopes, and Viana 2016; Godoi and Pujol-Luz 2018), see Supplementary Table 1 for the full information. In total, 69 stratiomyomorphan specimens were analyzed (see supplementary table 1, supplementary images).

**Deleted:** ... Rozkošný 2009; ... Marques and de Xerez 2009; Marshall 2012; ... Pujol-Luz and ... Pujol-Luz 2014a & b; Pujol-Luz, Lopes, and Viana 2016; ... Godoi and Pujol-Luz 2018), see Supplementary ... Table 1 for the full information. In total ... 69 stratiomyomorphan ...

Black and white outlines were produced using a polygonal tool and mask functionality of the program FIJI (Schindelin et al. 2012). Jpg outlines were analyzed in R using the *momocs* package (Bonhomme et al. 2014), with the shapes being characterized by 36 harmonics. Source code, list of the material used for the outline production, and all the underlying data are available as supplementary material (supplement 3). To estimate the habitat affinity of the fossil larvae, we plotted them into a single morphospace with the extant larvae. For the latter, we demarcated saproxylic, aquatic, and terrestrial habitats. Based on the position of the fossil larvae in this morphospace, we have attempted to assess their habitat affinity. All data analyses were conducted in R version 3.4.1 (2017-06-30) - "Single Candle" (R Core Team 2014).

**Deleted:** ... Jpg outlines were ... analyzed in R using the *momocs* package (Bonhomme et al. 2014), with the shapes being characterized by ... 36 harmonics. Source code, list of the material used for the outline production, and all the underlying data are available as supplementary material (supplement 3). To estimate the habitat affinity of the fossil larvae, we plotted them into ... a single morphospace ... with the extant larvae ... For the latter, we demarcated saproxylic, aquatic, and terrestrial habitats. Based on the position of the fossil larvae in this ... morphospace, we have attempted to assess their habitat affinity ...

#### Data availability

All the specimens used in the paper are deposited in public collections (see Table 1). All the outline jpg images are provided in the supplementary materials to this paper, together with the R code used to conduct the analysis.

#### Geological context

The geological context of Myanmar (Cruickshank and Ko 2003; Yu et al. 2019), Dominican (Iturralde-Vinent 2001) and Baltic (Wichard, Gröhn, and Sereduszus 2009) ambers, as well as Messel shale (e.g., Büchel and Schaal, 2018), has been explained in detail in various previous works.

**Deleted:** ¶

**Deleted:** ... Myanmar (Cruickshank and Ko 2003; Yu et al. 2019), Dominican (Iturralde-Vinent 2001) and Baltic (Wichard, Gröhn, and Sereduszus 2009) ambers, as well as Messel shale (e.g., Büchel and Schaal, 2018) ...

The Locality of Činžat is much less well known to the broader audience than the three above mentioned, so we are discussing it in further detail. The studied locality Činžat is situated in the Ribnica-Selnica graben (Jelen and Rifelj 2002) filled with sediments once deposited in the Central Paratethys sea (Rögl, 1998), within the westernmost parts of the Styrian Basin, approximately 15 km west of Maribor. Here, strata of the Ivnik Beds (Mioč 1972) are exposed in a belt from Maribor, on the northern slopes of the igneous Pohorje pluton, towards the town of Radlje.

**Deleted:**

**Deleted:** ...

Fossil bearing micaceous laminated siltstones cover older pre-Cenozoic rocks and sequences of loosely bound conglomerates, alternating with sandstones and siltstones of the Ivnik Beds. A late Burdigalian age (Miocene) coinciding with the 'Karpatian' stage of the regional scale was identified based on a benthic foraminifera association and nannoplankton sampling (Gašparič and Hyžný 2015).

The fossil fauna includes decapod crustaceans, bivalves, gastropods, and echinoids, which are randomly distributed within the siltstone layers of the Činžat section, although individual layers and variations in lithology are more likely to contain macrofaunal fossil remains. Interbedded layers of sandstones and conglomerates contain no macrofossils. The faunal association suggests low energy deep-water depositional environment with epibathyal water depth exceeding 125 m (Gašparič and Hyžný 2015).

## Results

We can distinguish six different morphotypes among the studied fossil larvae.

Description, general notes: To provide the reader, the necessary background, we first give a generalized description of the characteristics of larvae of Stratiomyidae (and to the same extent Stratiomyomorpha) segment by segment.

Deleted: reader

General shared appearance

Habitus. Small to medium-sized larva with slightly dorsoventrally flattened, spindle-shaped body. The body is fully covered with oval pellets, supposedly of calcium carbonate composition (although it is impossible to ascertain this aspect for the fossil forms conclusively) (Figs 1 A-B, 2 A-C, 3A-C, 4A).

Body length from 2 mm to slightly less than 20 mm. Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs 1A-B, 2 A-C, 4 A-C). Anterior segments are forming a distinct head capsule.

Head capsule sclerotized anteriorly, posterior part (one third to one half) reduced to several longitudinal structures, retracted into the anterior trunk (prothorax). The Head capsule is formed by the ocular segment plus five post-ocular segments.

Ocular segment recognizable by its appendage derivative, clypeo-labral complex.

Clypeus (clypeal sclerite) longer than wide. The labrum is roughly triangular, much longer than wide, strongly sclerotized (Figs. 2A-C, 3B, C). The segment with small stemmata ("eye prominences"), anteromedially.

Commented [TT2]: Need to re-write

Post-ocular segment 1, with a pair of antennae [antennulae in generalized terminology]. The antenna of Stratiomyomorpha larvae stout, comprising two elements, sitting in dorsoanterior position, or more towards the center of the dorsal surface of the head capsule. In many fossil specimens not preserved or not visible (Figs. 4B, C)

Post-ocular segment 2 (intercalary segment) without externally recognizable structures, not identifiable in the postembryonic development of most of the Diptera larvae. It might be argued, therefore, that discussion of such seemingly absent structure in the description is unnecessary, or mixing conjectures with observed structures. We will say, for the contrary, however. The reason is that there is the knowledge and hence expectation of the presence of this segment based on prior knowledge. Yet, we do not see it. In broader comparison, this is, in fact, informative and needs to be included in the taxa description. Post-ocular segments 3 and 4 were recognizable by their appendage's mandibles and maxillae [maxillula in generalized terminology]. Mandibles and maxillae form a single compound, the mandibular-maxillary

Deleted: structures,

Commented [TT3]: This is too wordy - need to trim

Deleted: ¶

Deleted: appendages

Commented [TT4]: [ ] not ( ) .... why?

complex (autapomorphy of Stratyomyomorpha); comprising elements largely indistinguishable, apart from the distal parts of the maxillae (maxillary palp). Maxillary palps quite stout, but prominent (Schremmer 1951, Rozkošný 1981). The proximal part of the mandibular-maxillary complex, fully sclerotized; with strong, multi-branched setae on its dorsodistal surface, as well as laterally. Distal part or palp, conical, with two elements (palpomeres). Apical part of the mandibular-maxillary complex bears an arrangement of the setae ("brush") of varying complexity (autapomorphy of Stratyomyomorpha). Basal part bearing a ventral "grinder", which is heavily sclerotized (Figs. 3A-C, 4B, C). On the ventral side, mandibular-maxillary complex forms ventral plates, occupying the ventral side of the head capsule (Sinclair 1992).

Trunk (thorax+abdomen) with eleven visible units, interpreted as 3 thorax segments, 7 abdominal segments and a trunk end (abdomen unit 8). Cuticle covered with round deposits of calcium carbonate pellets, forming a honeycomb-like pattern (autapomorphy of Stratyomyomorpha). Remark: It is difficult to ascertain that the cuticle of the fossils is indeed covered in calcium carbonate pellets. It cannot be excluded that such cuticle scales are simple chitin as in larvae of the Ephydriidae or Oestridae (Marshall 2012).

Trunk units without any parapods, creeping welts or protuberances. Different arrangements of spiracles possible: 1) Trunk bears nine pairs of spiracles (openings of the tracheal system): one pair of spiracles on prothorax, and eight pairs on the posterior trunk (abdomen). This type of the tracheal system is called peripneustic (Hennig, 1952). 2) most spiracles reduced, amphipneustic (spiracles present on prothorax and trunk end) or 3) methapneustic (spiracles on trunk end only) (McFadden 1967) (Figs 2A-C, Supplementary figures 4A-D).

Anterior trunk or thorax with three segments, pro-, meso- and methathorax. Armament represented by the calcium carbonate pellets and large rhombic sclerites on the sternites, occasionally with some modified, spike-like setae. Prothorax with 2–3 pairs of anterodorsal setae (Rozkošný 1981).

Mesothorax and metathorax with numerous dorsal and ventral setae as well as numerous pellets of calcium carbonate (Figs. 1A, B). All three units (= segments in this case) of the anterior trunk (thorax) are having very uniform setation. Each of the thoracic segments bears three pairs of dorsal setae (D1–D3), one pair of dorsolateral setae, and one pair of ventrolateral setae. Additionally, each thoracic segment bears two pairs of ventral setae (Figs 1 A, B). Inner pair of ventral setae simple, outer pair contains several branched setae. The latter also is known as a "thoracic leg group" setae (Rozkošný 1981).

Posterior trunk (abdomen) units 1–7 with setae arranged in a uniform pattern. This pattern includes three pairs of dorsal setae, in addition to a single pair of dorsolateral and a pair of ventrolateral setae on each of the abdominal unit. Each of these units also bear one or two pairs of lateral setae. These lateral setae can be quite prominent. Additionally, three (sometimes four) pairs of ventral setae arranged in a transverse row on the sternites of abdominal units 1–7 (Rozkošný 1981). Trunk end (abdomen unit 8) bears two pairs of lateral setae, which often are quite long. Additionally, trunk end bears one pair of subapical setae, and one pair of apical setae.



Setae of both groups are usually quite short. Dorsal setae are present but rarely prominent on the trunk end. Large anal cleft (anus) present on ventro-terminal part of the trunk end. Around this cleft ventral setae arranged in five pairs, situated along and behind anal cleft (Fig. 1B) (Rozkošný 1981).

Deleted: this cleft ventral setae

## Summary of main results

In total we can distinguish six different morphotypes among the studied fossil larvae.  
Morphotype 1 (Stratiomyomorpha)

Material examined: 13 specimens (PED-0025, PED-0031\_1, PED-0031\_2, PED-0031\_3, PED-0031\_4, PED-0041, PED-0113, PED-0152\_1, PED-0152\_2, PED-0152\_3, PED-0243, PED-0349, PED-0362) in 8 amber pieces (see Table 1, Supplementary fig. 1). Most of the measurement were performed on the two best preserved specimens PED-0031\_1 and PED-0041 (Figs. 2 A-C, 3 A-C, 4A-C, Supplementary figures 1,2, 3, 4, 5, 6, 7). Syninclusions: see Table 1.

Deleted: ...

## Description:

Habitus. Medium sized larva with slightly dorsoventrally flattened, spindle shaped body, fully covered with oval pellets or scales (Figs. 2 A-C, 4A).

Deleted: ... dorsoventrally flattened, spindle shaped body, fully covered with oval ... pellets or scales (Figs. ... 2 A-C, ... 4A).

Body length 2.3-1.1 mm (n=9). Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 2 A-C, 4A). Anterior segments forming distinct head capsule.

Deleted: ... 2 A-C, ...

Head capsule sclerotized anteriorly, posterior part reduced to several longitudinal structures (unpaired metacephalic rod, paired tentorial arms) retracted into the anterior trunk (prothorax and mesothorax). Dimensions of head capsule (including metacephalic rod and the tentorial arms protruding far back into the prothorax (Figs. 4A-C).

Deleted: ... Figs. ...

Ocular segment recognizable by its appendage derivative, clypeo-labrum complex.

Clypeus (clypeal sclerite) longer than wide. Labrum roughly triangular, much longer than wide, strongly sclerotized (Figs. 3A-C, 4B, C). Segment with small apparent stemmata, posterolaterally.

Deleted: ... recognizable by its appendage derivative, clypeo-labrum complex. Clypeus ( ... clypeal sclerite) longer than wide. Labrum roughly triangular, much longer than wide, strongly sclerotized (Figs. 3A-C, 4B, C). Segment with small apparent stemmata, ... posterolaterally.

Post-ocular segment 1 recognizable by its pair of appendages, antenna [antennula].

Antenna prominent, robust 25 µm long (n=1) (Figs. 4B, C)

Deleted: ... recognizable by its pair of appendages, antenna antenna [antennula]. Antenna prominent, robust 25 µm long (n=1) (Figs. ... 4B, C)

Post-ocular segment 2 (intercalary segment) without externally recognizable structures.

Post-ocular segments 3 & 4 recognizable by its pair of appendages -, mandibular-maxillary complex (Figs. 2A-C, 3A-C). Proximal part of fully sclerotized with strong, multi-branched setae on the dorsodistal surface, as well as laterally. Distal part, palp, conical, with two elements (palpomeres -). Basal part of the complex bearing a large molar "grinder", which is occupying almost entire ventral side of the head capsule and heavily sclerotized (Figs. 2A-C, 3B, C).

Deleted: ... segments 3 ... & 4 recognizable by its pair of appendages ... -; mandibular-maxillary complex ... Figs. 2A-C, 3A-C ... Proximal part of ... fully sclerotized with strong, multi-branched setae on the ... dorsodistal surface, as well as laterally. Distal part, palp, conical, with two elements (palpomeres ...). Basal part of the ... complex bearing a large ...

Post-ocular segment 5 recognizable by its appendages, forming the labium, represented by a fleshy lobe.

Deleted:

Trunk (thorax+abdomen) with 11 visible units, interpreted as 3 thorax segments, 7 abdomen segments and a trunk end (abdomen unit 8). Trunk is yellowish-brown, except for the very first unit which is light-yellow. Cuticle is covered with oval pellets or scales. Units of the posterior trunk do however bear complex armament on dorsal and ventral sclerites (tergites and sternites; Figs. 1A-C).

Anterior trunk, thorax with three segments, pro-, meso- and metathorax.

Deleted: ... Anterior trunk, thorax with three segments, pro-, meso- and ...

Prothorax 450-770  $\mu\text{m}$  long (n=2), without protrusions. Armament represented by oval pellets or scales and large rhombic sclerite on the sternite, with two rows of small, flat spikes arranged anteriorly on sternite. Distinct spiracle (anterior spiracle) on shallow depression at the posterolateral part of the prothorax (Figs 1A-C).

Deleted: ... oval pellets or scales and large rhombic sclerite on the sternite, with two rows of small, flat spikes arranged anteriorly on sternite. Distinct spiracle (anterior spiracle) on shallow depression at the ...

Mesothorax yellowish-brown, 360-540  $\mu\text{m}$  long (n=2). With two rows of triangular, flat spines on the anterior edge of sternite. Numerous oval pellets or scales.

Deleted: ...

Metathorax yellowish-brown, 400-660  $\mu\text{m}$  long (n=2), bears two rows of triangular, flat spines on the anterior edge of sternite, as well as numerous oval pellets or scales.

Deleted: ... triangular, flat spines on the anterior edge of sternite, as well as numerous ...

Posterior trunk, abdomen with 8 distinct units. Anterior seven representing true segments.

Abdomen unit 1 rectangular in dorsoventral plain, 440-760  $\mu\text{m}$  long (n=2). Bearing numerous oval pellets or scales, as well as two rows of the small triangular spikes on the anterior edge of the sternite. Posterior edge of dorsal sclerite, tergite, with a row of 12 very strong dorsoventrally triangular spines.

Deleted: ... dorsoventral plain, 440-760  $\mu\text{m}$  long (n=2). Bearing numerous ... oval pellets or scales, as well as two rows of the small triangular spikes on the anterior edge of the sternite. Posterior edge of dorsal sclerite, tergite, with a row of 12 very strong, ...

Abdomen units 2-7 rectangular (370-920  $\mu\text{m}$  long). Bearing numerous oval pellets or scales. Posterior edge of dorsal sclerites, tergites, each with a row of very strong triangular spines, 10-12 such spines on abdomen units 2-6, 7 on abdomen unit 7.

Deleted: ...

Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) roughly trapezoid in the dorsoventral view, 620-750  $\mu\text{m}$  long (n=2). With three pairs of small lateral setae, two pairs of strong black setae on two mounds at the middle of tergite; two pairs of strong needle-like setae on two smaller mounds at the distal edge of on dorsal tergite (syn-tergite?). Tergite also bears posterior spiracles in a transversal cleft, ventrally. Large, transversal anal cleft, surrounded by an elevated oval sclerotized area, of markedly darker color than the rest of the cuticle visible at trunk end.

Deleted: ... dorsoventral view, 620-750  $\mu\text{m}$  long (n=2). With three pairs of ... small lateral setae, two pairs of ... strong black setae on two mounds at the middle of tergite; ... two pairs of strong needle-like setae on two smaller mounds at the distal edge of on dorsal tergite (syn-tergite?). Tergite also bears posterior spiracles in ... a transversal cleft, ventrally. ... Large, transversal anal cleft, surrounded by ... an elevated oval sclerotized area, of markedly darker color than the rest of the cuticle ...

Morphotype 2 (Stratiomyomorpha: Stratiomyidae)

Material examined: LACM ENT 366281(5 specimens in a single piece). Most measurements are based on a single specimen, well preserved and visible in dorsal aspect. (Figs. 5A-B, 6 A-D, Supplementary figure 8 A-B).

Deleted: ... measurements are based on a single specimen, specimen, well preserved and visible in dorsal aspect. (Figs. ... 5A-B, ...

Syninclusions: N.A.

## Description:

Habitus. Medium sized larva with somewhat dorsoventrally flattened, spindle shaped body, covered with oval pellets of the calcium carbonate (Figs. 5 A-B).

Body covered by white film, precluding observation of many fine details. Length 3.3-3.7 mm (n=3). Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 5 A-B, Supplementary figure 8 A, B). Anterior segments forming distinct head capsule.

Head capsule sclerotized anteriorly, posterior part reduced to several longitudinal structures (unpaired metacephalic rod, paired tentorial arms), retracted into prothorax. Dimensions of head capsule: 480 µm long, 340 µm wide (n=1).

Surface of head capsule covered with pellets of calcium carbonate (Figs. 6 A-D).

Ocular segment recognizable by its appendage derivative, clypeo-labral complex.

Clypeus (clypeal sclerite) fused with the frontal sclerite. Labrum roughly beak-like (100 µm long, 70 µm wide), much longer than wide, strongly sclerotized (Figs. 6 A-D). Segment with small apparent stemmata, anterolaterally.

Post-ocular segment 1: not externally recognizable, possible structures (antennae) not apparent.

Post-ocular segment 2 (intercalary segment) without externally recognizable structures.

Post-ocular segments 3 & 4 recognizable by their pairs of appendages forming mandibular-maxillary complex (Figs. 6 A-D). Distal lobe brown in color, distal ends chisel-like. Palp (distal part) not visible on any of the specimens available. (Figs. 5A-D).

Post-ocular segment 5 not recognizable, its appendages, presumably forming the labium, not visible in any of the specimens available (Figs. 6A-D).

Trunk (thorax+abdomen) with 11 visible units, interpreted as 3 thorax segments, 7 abdomen segments and trunk end (abdomen unit 8). Trunk is yellowish-brown, except for the very first unit which is light-yellow. Cuticle is covered with round deposits of calcium carbonate pellets. Trunk dorsoventrally flattened, spindle-shaped, total length 1.9-2.7 (n=3) mm long; densely covered with oval pellets or scales (Figs. 5 A-B, Supplementary figure 8 A, B). Anterior trunk, thorax with three segments, pro-, meso- and metathorax.

Prothorax, ring-like, 240µm long, 630 µm (n=1), wide, with ventral excision at place of head capsule insertion. Small spiracles on posterolateral surface. Prothorax bears no protrusions. Armament represented by oval pellets or scales. Anterior spiracle sits on conical protrusion, ca. 35 µm long, spiracle itself with a single longitudinal opening (Figs. 5 A-B, Supplementary figure 8 A, B).

Mesothorax 110 µm long, 780 µm wide (n=1), ring-shaped, with no visible protrusion, bearing numerous oval pellets or scales.

Metathorax 180 µm long, 820µm wide (n=1), ring shaped, with one pair of the long, wavy setae.

Posterior trunk, abdomen with 8 distinct units. Anterior seven representing true segments.

**Deleted:** ... dorsoventrally flattened, spindle shaped body, covered with oval ... pellets of the calcium carbonate (Figs. ...)

**Deleted:** ... many fine details. Length 3.3-3.7 mm (n=3). Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. ...)

**Deleted:** ... longitudinal structures (unpaired metacephalic rod, paired tentorial arms), retracted into ...

**Deleted:** ... pellets of calcium carbonate (Figs. ... 6 A-D ...)

**Deleted:** ... recognizable by its appendage derivative, clypeo- ... labral complex. Clypeus ( ... clypeal sclerite) fused with the frontal sclerite. Labrum roughly beak-like (100 µm long, 70 µm wide), much longer than wide, strongly sclerotized (Figs. ...)

**Deleted:** ... recognizable, possible structures (antennae) not not ...

**Deleted:** ... segments 3 ... & 4 recognizable by ... their pairs of appendages ... forming mandibular-maxillary complex ... (Figs. 6 A-D). Distal lobe brown in ...

**Deleted:** ... , not visible in any of the specimens available (Figs. ...)

**Deleted:** ... Trunk (thorax+abdomen) with 11 visible units, interpreted as 3 thorax segments, 7 abdomen segments and trunk end (abdomen unit 8). Trunk is yellowish-brown, except for the very first unit which is light-yellow. Cuticle is covered with round deposits of calcium carbonate ... pellets. Trunk dorsoventrally flattened, spindle-shaped, total length 1.9-2.7 (n=3) mm long; densely covered with ...

**Deleted:** ...

**Deleted:** ... ventral excision at place of ... head capsule insertion. Small spiracles on ... posterolateral surface. Prothorax bears no protrusions. Armament represented by ... oval pellets or scales. Anterior spiracle sits on ... conical protrusion, ca. 35 µm long, spiracle itself with a single longitudinal opening (Figs. ...)

**Deleted:** ... -shaped, with no visible protrusion, bearing numerous oval ...

**Deleted:** ...

Abdomen units 1-7 wider than long (200-260  $\mu\text{m}$  long; 900-1000  $\mu\text{m}$  wide). All units bearing several wavy lateral setae; unit 7 additionally bears two lateral wavy setae.

Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) roughly square shaped in dorsal or ventral view, (502  $\mu\text{m}$  long, 525  $\mu\text{m}$  wide); with two pairs of the large, wavy setae. Anal cleft sitting on large elevated mounds posteriorly on tergite (Figs. 5 A-B, Supplementary figure 8 A, B).

Morphotype 3 (Stratiomyomorpha: Stratiomyidae)

Material examined: Piece of Dominican amber with a single fossil larva from the PED collection (collection number PED-0001; Figs. 7 A-B, 8 A-D, 9, Supplementary figures 9 A-B, 10 A-B). The larva is well preserved, anterior trunk obscured ventrally by a large air bubble. Head capsule details inaccessible.

Description:

Habitus. Medium-sized larva with dorsoventrally flattened body, and triangular posterior end in the dorsoventral plain (Figs. 7 A-B, 8 A-B, 9). Body armoured with oval pellets or scales. Total length 9.5 mm. Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 7 A-B). Anterior segments forming distinct head capsule.

Head capsule partially sclerotized, longer than wide, posterior part of the head capsule is retracted into the trunk. Dimensions of head capsule: 720  $\mu\text{m}$  long, 550  $\mu\text{m}$ . Surface of head capsule covered with small cuticular scales with oval pellets or scales (Fig. 7A-B).

Ocular segment recognizable by its appendage derivative, clypeo-labral complex. With 2 pairs of setae, 2 labral setae and 2 frontoclypeal setae. Clypeus continuous with labrum, clypeus narrow, labrum expanding distally (Figs. 8A, C). Segment with pair of apparent stemmata (larval eyes).

Post-ocular segment 1 recognizable by its pair of appendages, antennae [antennula], inserting ventrolaterally at the anterior end of the head capsule (Figs. 8B). Antenna short, consists of two elements.

Post-ocular segment 2 (intercalary segment) without externally recognizable structures.

Post-ocular segments 3 & 4 recognizable by its pair of appendages, mandibular-maxillary complex. Proximal heavily sclerotized, with basal plates. Main part lobe hook-shaped, continuous with appendages of the following post-ocular segment, integrated into the mandibular-maxillary complex. Inner surface forms longitudinal striated "molar" area (Figs. 8A, B). Distal lobe fleshy, with numerous maxillary setae (Figs. 8A, B).

Post-ocular segment 5 recognizable by its appendages, forming the labium. Labium bearing 3 pairs setae (2 ventral setae and 4 ventrolateral). Proximal part of labium forms a funnel connected to oral cavity. Labium distally with 2 projections, probably palps. Labium highly modified, connected to cibarial (pharyngeal) skeleton of the head capsule (Fig. 8A, B).

Trunk (thorax+abdomen) with 11 visible units, interpreted as 3 thorax segments, 7 Abdominal units and a trunk end (abdominal segment 8) (Figs. 7 A-B, 8A-D, Supplementary figures 9 A-B, 10 A-B). Trunk spindle shaped in a dorsoventral plain, parallel sided in the

**Deleted:** ... (abdomen unit 8, undifferentiated abdomen segments ... 8-11?) roughly square shaped in dorsal or ventral view, (502  $\mu\text{m}$  long, 525  $\mu\text{m}$  wide); with two pairs of the large, wavy setae. ... Anal cleft sitting on large elevated mounds posteriorly on ... tergite ... (Figs. ... )

**Deleted:**

**Deleted:** ... 7 A-B, ... 8 A-D, 9, Supplementary figures 9 A-B, 10 A-B). The larva is well preserved, anterior trunk obscured ventrally by a large air bubble. ...

**Deleted:** ... Habitus. Medium ... -sized larva with ... dorsoventrally flattened body, and triangular posterior end in the ... dorsoventral plain (Figs. 7 A-B, 8 A-B, 9). Body armoured with ... oval pellets or scales ... Total length 9.5 mm. Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 6...

**Deleted:** ... Head capsule partially sclerotized, longer than wide, posterior part of the head capsule is retracted into the trunk. Dimensions of head capsule: 720  $\mu\text{m}$  long, 550  $\mu\text{m}$ . Surface of head capsule covered with small cuticular scales with ...

**Deleted:** ... recognizable by its appendage derivative, clypeo- ... labral complex. With 2 pairs of setae, 2 labral setae and 2 ... frontoclypeal setae. Clypeus continuous with labrum, clypeus narrow, labrum expanding distally (Figs. 5...

**Deleted:** ... recognizable by its pair of appendages, antennae [antennula], inserting ... ventrolaterally at the anterior end of the head capsule (Figs. 7...

**Deleted:** ... segments 3 ... & 4 recognizable by its pair of appendages, ... mandibular-maxillary complex. Proximal heavily sclerotized, with basal plates. Main part ... lobe hook-shaped, continuous with appendages of the following post-ocular segment, integrated into the mandibular-maxillary complex. Inner surface forms longitudinal striated "molar" area (Figs. 87... B). Distal lobe fleshy, with numerous maxillary setae (Figs. 87...

**Deleted:** ... Post-ocular segment 5 recognizable by its appendages, forming the labium ... Labium bearing 3 pairs setae (2 ventral setae and 4 ... ventrolateral). Proximal part of labium forms a funnel connected to ... oral cavity. Labium distally with 2 projections, probably palps. Labium highly modified, connected to ... cibarial (pharyngeal) skeleton of the head capsule (Fig. 87...

**Deleted:** 6 A-B, 87. ...-D, Supplementary figures 9 A-B, 10 A-B). B). Trunk spindle shaped in a ...

middle region, triangular at the hind-end. All bearing oval pellets or scales, also with many long setae.

Anterior trunk, thorax with three segments, pro-, meso- and metathorax. Thoracic "leg" setae groups seemingly with 2 setae in each group (Figs. 7 A-B, 9, Supplementary figures 9 A-B, 10 A-B).

Prothorax 760  $\mu\text{m}$  long. Prothorax with numerous setae: 4 antero-dorsal, 6 dorsal, 2 dorsolateral, 4 lateral, 2 ventrolateral and 6 ventral (Figs. 7 A-B, Supplementary figures 9 A-B, 10 A-B). Prothorax bears a pair of spiracles.

Mesothorax 800  $\mu\text{m}$  long, with numerous setae: 6 dorsal, 2 dorsolateral, 4 lateral, 2 ventrolateral and 6 ventral.

Metathorax 500  $\mu\text{m}$  long, with numerous setae: 6 dorsal, 2 dorsolateral, 4 lateral, 2 ventrolateral and 6 ventral setae (Figs. 6 A-B, Supplementary figures 9 A-B, 10 A-B).

Posterior trunk (abdomen) with 8 apparent units flattened dorsoventrally, mostly oval in the dorsal plain, with triangular posterior hind-end, (Figs. 7 A-B, 9). Abdomen units 1-7 with numerous setae: 6 dorsal setae, 2 dorsolateral setae, 4 lateral setae, 2 ventrolateral setae 4 ventral, on each segment (Figs. 7 A-B, Supplementary figures 9 A-B, 10 A-B). Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) triangular in general shape, dorsoventrally, bears well visible anus on the ventroterminal part. Carries numerous setae: ventral setae pairs v1 through v4, two pairs of anal setae and 8 dorsolateral setae. Terminal end elongated into the two rod-shaped protrusions, each carrying anal setae. No cuticular "teeth" along anal opening (Fig. 7 A, B).

Morphotype 4 (Stratiomyomorpha: Stratiomyidae ex)

Material examined: small slab of the Činžat shale with a cuticular fossil of a larva. Specimen split in half along the medio-lateral surface of the sternites, so that tergites of the posterior trunk (units 5-8) are folded upon the tergites of the more anterior ones (1 ex -4 ex). Coloration of specimen very well preserved (Figs. 10 A-B, 11 A-D, Supplementary figure 12 A-B, 13 A-D).

Description:

Habitus. Medium sized larva with dorsoventrally flattened body and rounded posterior end. Body armored with oval pellets or scales. Total length 6.4 mm. Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 10 A-B ex). Anterior segments forming distinct head capsule.

Anterior body visible in ventral perspective only, of the posterior body also the dorsal region can be seen. Body with distinct sclerites ventrally on anterior trunk, as well as dorsally on posterior trunk, bearing distinctly "leopard" pattern of coloration, consisting from the dark-grey and brownish -yellow spots of the irregular shape ( ex Figs. 10 A-B, Supplementary figure 12 A-B ex ).

Head capsule sclerotized, much longer than wide, posterior part of the head capsule is retracted into the trunk. Dimensions of head capsule: 1000  $\mu\text{m}$  long, 250  $\mu\text{m}$ . Figs. 11 A-D, Supplementary figure 13 B).

Deleted: ...

Deleted: ...metathorax. Thoracic "leg" setae groups seemingly with 2 setae in each group (Figs. 76...

Deleted: ...ventrolateral and 6 ventral (Figs. 76

Deleted: ...

Deleted: ...dorsolateral, 4 lateral, 2 ...

Deleted: ...dorsoventrally, mostly oval in the dorsal plain, with triangular posterior hind-end, (Figs. 76...A-B, 9). Abdomen units 1-7 with numerous setae: 6 dorsal setae, 2 ... dorsolateral setae, 4 lateral setae, 2 ... ventrolateral setae 4 ventral, on each segment (Figs. 76...A-B, Supplementary figures 9 A-B, 10 A-B). Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) triangular in general shape, ... dorsoventrally, bears well visible anus on the ... ventroterminal part. Carries numerous setae: ventral setae pairs v1 through v4, two pairs of anal setae and 8 ... dorsolateral setae. Terminal end elongated into the two rod-shaped protrusions, each carrying ... anal setae. No cuticular "teeth" along anal opening (Fig. 76...

Deleted:

Deleted: ...posterior trunk (units 5-8) are folded upon the tergites of the more anterior ones (1 ... -4 ... ). Coloration of specimen very well preserved (Figs. ... 109...A-B, ... 110...

Deleted: ...dorsoventrally flattened body ... and rounded posterior end. Body ... armored with ... oval pellets or scales. Total length 6.4 mm. Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. ... 109...A-B ...

Deleted: ...perspective only, of the posterior ... body also the dorsal region can be seen. ... Body with distinct sclerites ventrally on anterior trunk, as well as dorsally on posterior trunk, bearing distinctly "leopard" pattern of coloration, consisting from the dark-grey and brownish -yellow spots of the irregular shape ( ... Figs. 109...A-B, Supplementary figure 12 A-B ...

Deleted: ...110

Ocular segment Ocular segment recognizable by its appendage derivative, clypeo-labral complex. Clypeus continuous with labrum, clypeus narrow, blade-shaped (Figs. 11 A-D). With pair of apparent hemispherical stemmata (larval eyes), at about mid length of the head capsule, dorsolaterally. Segment surface bears multiple small setae.

**Deleted:** ...recognizable by its appendage derivative, clypeo- ... labral complex. Clypeus continuous with labrum, clypeus narrow, blade-shaped (Figs. ...110...A-D). With pair of apparent hemispherical stemmata (larval eyes), at about ...mid length of the ...

Post-ocular segment 1 recognizable by its pair of appendages, antennae [antennula]. Antenna inserted dorsolaterally at the distal end of the head capsule (Figs. 11 A-D, Supplementary figure 13 B). Antenna short, with two elements.

**Deleted:** ...recognizable by its pair of appendages, antennae [antennula]. Antenna inserted ... dorsolaterally at the distal end of the head capsule (Figs. ...110...

Post-ocular segment 2 (intercalary segment) without externally recognizable structures.

Post-ocular segments 3 & 4 recognizable by its pair of appendages, forming the mandibular-maxillary complex. Complex with a proximal lobe, heavily sclerotized, with basal plates; the main part is a lobe hook-shaped, continuous with appendages of the following post-ocular segment. Inner surface forms longitudinal striated "molar" area (Figs. 11 A-D, Supplementary figure 13 B). Distally with fleshy lobe, with numerous setae (Fig. 11 A).

**Deleted:** ...segments 3 ... & 4 recognizable by its pair of appendages, ... forming the ... mandibular-maxillary complex. ... Complex with a proximal lobe, heavily sclerotized, with basal plates ... the main part ... is a lobe hook-shaped, continuous with appendages of the following post-ocular segment. Inner surface forms longitudinal striated "molar" area (Figs. ...110...A-D, Supplementary figure 13 B). Distally with fleshy lobe, with numerous setae (Fig. 110...

Post-ocular segment 5 recognizable by its pair of appendages, forming the labium. Labium bears 3 pairs setae (2 ventral setae and 4 ventrolateral), on the ventral and lateral surface respectively. Proximal part of labium forms a three-pronged structure, adjacent to the oral cavity (Figs. 10 A-D, Supplementary figure 13 B).

**Deleted:** ... Post-ocular segment 5 recognizable by its pair of appendages, forming the labium ... Labium bears 3 pairs setae (2 ventral setae and 4 ... ventrolateral), on the ventral and lateral surface respectively. Proximal part of labium forms a three-pronged structure, adjacent to the oral cavity (Figs. 109...

Trunk (thorax+abdomen) with 11 visible units, interpreted as 3 thorax segments, 7 abdomen segments and a trunk end (abdomen unit 8). Trunk bears 2 pairs of spiracles (openings of the tracheal system) (Figs. 10 A-B, Supplementary figure 12 A-B, 13 A, B).

**Deleted:** ...bears 2 pairs of spiracles (openings of the tracheal system ... ) (Figs. 109...A-B, Supplementary figure 12 A-B ... , 13 A, B).

Anterior trunk (thorax) consists of three segments, pro-, meso- and metathorax. Tergites and sternites sclerotized, bearing oval pellets or scales.

**Deleted:** ... (thorax) consists of three segments, pro-, meso- meso- and metathorax. Tergites and sternites sclerotized, bearing ...

Prothorax 300 µm long. Bears a pair of large spiracles (100 µm in diameter at the opening). Prothorax with several small setae on the dorsal surface (Figs. 10 A-B, Supplementary figure 12 A-B, 13 A, B).

**Deleted:** ... opening). Prothorax with several small setae on the dorsal surface (Figs. 108...A-B, Supplementary figure 12 A-B ...

Mesothorax 300 µm long, ring-shaped, bearing no spiracles, with lighter area in the center of the sternite (probably due to the sediment filling the depressions of the fossil).

**Deleted:** ... lighter area in the ... centre...enter of the sternite (probably due to the sediment filling the depressions of the fossil ...

Metathorax 250 µm, ring-shaped, with the lighter area in the centre of the sternite (probably due to the sediment filling the depressions of the fossil).

**Deleted:** ...

Posterior trunk, abdomen with 8 distinct units. Anterior seven units representing true segments. Posterior trunk mostly oval with rounded posterior hind-end (Figs 10 A-B, Supplementary figure 12 A-B, 13 A, B).

**Deleted:** 8Figs 10 A-B, Supplementary figure 12 A-B ...

Abdomen units 1-7 (320-610 µm long). Cuticle is split along the lateral side, medio-laterally; therefore units 5-7 (and trunk end) folded over the ventral parts of the units 1-4. This damage reveals the inner dorsal surface of abdomen units 5-7 (and trunk end) for the direct observation.

Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) semicircular in general shape in dorsoventral view; bears anus on ventroterminal part. No cuticular "teeth" along anal opening (Figs. 10 A-B, Supplementary figure 13 C).

**Deleted:** ... in ... dorsoventral view; bears anus on on ... ventroterminal part. ... No cuticular "teeth" along ... anal opening (Figs. 108...



## Morphotype 5 (Stratiomyomorpha: Stratiomyidae: Stratiomyinae)

Material examined: a single fossil larva in a piece of Baltic amber from the PED collection (collection number PED- 7568-100). The larva is poorly preserved, covered with air bubbles and cracks in amber; only rear end of the trunk visible well enough to provide any distinguishable features (Figs. 12 A - B). Piece of amber contains several syninclusions: non-biting midge male (Diptera, Chironomidae); window-gnat (Diptera, Anisopodidae), two dark-winged fungus gnats (Diptera, Sciaridae), large spider (Araneae).

Description:

Habitus. Medium sized larva with spindle shaped body in dorsoventral view, end of trunk with prominent coronet of large setae. Body mostly obscured by cracks and bubbles in the amber; only rear end clearly visible. Total length 4.3 mm. Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs 12 A - B).

Trunk (thorax+abdomen) spindle shaped, parallel sided, rounded at the hind-<sup>xy</sup> end in dorsoventral view. Anterior part of the trunk entirely obscured by cracks.<sup>xy</sup> Subdivision of units<sup>xy</sup> unclear. Posterior trunk<sup>xy</sup> bear densely<sup>xy</sup> arranged strong setae. Trunk end (undifferentiated abdominal segments 8-11?) rounded in general shape, carries strong coronet formed by 19 unbranched setae (Figs.<sup>xy</sup> 12 A - B). Additionally<sup>xy</sup> bears a pair of large spiracles, surrounded by<sup>xy</sup> this coronet of setae and upper and lower sclerotized "lips"<sup>xy</sup>

## Morphotype 6 (possibly Stratiomyomorpha: Stratiomyidae)

Material examined: two fossil larvae on one slab from the Grube Messel, stored in the S.F. collection (collection number SF-MeI 4666; Figs. [13](#) A-C). The fossils originate from the Messel Formation, they were collected in the year 1994 in grid square E8, 0.9m to 1.1m below local stratigraphic marker horizon alpha. The larvae are poorly preserved, only traces of the head capsules and the rest of the bodies can be seen; no traces of any setae are preserved; nevertheless, both specimens show a well-preserved coloration pattern of the tergites.

Description:

**Habitus.** Medium sized larva with spindle shaped body. Accessible only in dorsal aspect.

Body length 3.0 to 3.5 mm (n=2). Body differentiated into presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 13A-C). Anterior segments forming distinct head capsule.

Head capsule partially sclerotized, longer than wide, posterior part of the head capsule retracted into the anterior trunk (prothorax). Head capsule visible only in vague outlines, with several longitudinal structures (unpaired metacephalic rod, paired tentorial arms), these are heavily sclerotized. Posterior part of the head capsules more heavily sclerotized (Figs. 13A-C). Width of head capsule ca. 270µm. Other units of the body difficult to measure due to the poorly visible borders between the segments.

Anterior segments not well apparent, without prominent structures.

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

Deleted.

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

**Deleted:**

100

Post-ocular segment 5 recognizable by an internally located pharyngeal grinding mill (visible in both fossil specimens; Fig. 13C).

Trunk (thorax+abdomen) spindle-shaped, parallel-sided, rounded at the hind-end. With eleven units: three thorax segments, 7 abdomen segments plus trunk end. Units of the trunk are much wider than long. No setae preserved. No traces of spiracles or a distal coronet of setae present (Fig. 13C).

Anterior trunk, thorax, consisting of pro-, -meso and metathorax.

Prothorax with general outlines visible; heavily sclerotized posterior part of the head capsule can be seen retracted into prothorax (Fig. 13A-C).

Mesothorax bears two distinct pigment dots at the hind edge (Fig. 13A, C).

Metathorax bearing no spiracles (Fig. 13A-C).

Posterior trunk (abdomen) with 8 units (Fig. 13A-C).

Abdomen units 1-6 bearing distinct lines of pigmentation, 2 medially on all tergites, and 2 laterally on most tergites (Fig. 13A-C).

Abdomen unit 7 preserves no details, only general outlines can be seen (Fig. 13A-C).

Trunk end (Abdominal unit 8) only general outline can be seen; square in general shape, with a rounded posterior edge, when viewed in the dorsoventral view (Fig. 13A-B). No spiracles or anus can be discerned.

## Discussion

### Systematic interpretation

All specimens can easily be identified as larval forms of Diptera. This interpretation can be based on the general body shape of the specimen, the absence of walking ("ambulatory") legs on the thorax, as well as the spiracle arrangement. The six morphotypes differ in numerous characters; their systematic relationships are discussed.

*Morphotype 1:* This morphotype is interpreted to be a representative of the group soldier and timber flies (Stratiomyomorpha) based on the following combination of characters (see Figs. 1A-C, 2 A-C, 3 A-C, Supplementary figures 1, 2, 3, 4, 5, 6, 7): larva elongated and flattened, with head, thorax and 8 abdominal units; body with oval pellets or scales, resembling calcium carbonate scales; presence of such scales is a synapomorphy of Stratiomyidae+Xylomyidae (Figs. 2A-C, 3 A-C, 4 A-C, Supplementary figures 1, 2, 3, 4, 5, 6, 7). The thorax of these specimens bears oval pellets or scales, rather than hardened sclerites as in Xylomyidae (Fig. 2B). Mandibles and maxillae are conjoined into a mandibular-maxillary complex (Fig. 4B, C). Larvae possess a large molar grinder and a setal brush at this mandibular-maxillary complex (Figs. 4B, C). The Brush of the mandibular-maxillary complex, as indeed complex itself, is substantially reduced and simplified (Figs. 4B, C). This condition is, however, not uncommon among extant representatives of Stratiomyidae, for example in mature larvae of Hermeteiinae and Sarginae (Rozkošný 1981).

Deleted: ...recognizable by an internally located pharyngeal grinding mill (visible in both fossil specimens; ...)

Deleted: ...With eleven units: three thorax segments ... , 7 abdomen segments plus trunk end. Units of the trunk are much wider than long. No setae preserved. No traces of ... spiracles or ... a distal ... coronet of setae present (Fig. 131...). ...

Deleted: 1

Deleted: 1

Deleted: 1

Deleted: 1A-C). ...

Deleted: ... Abdomen units 1-6 bearing ... distinct lines of pigmentation, 2 medially on all tergites, and 2 laterally on most tergites (Fig. 131...)

Deleted: ... Abdomen unit 7 preserves no details, only general outlines can be seen (Fig. 131...)

Deleted: ... dorsoventral view (Fig. 131)

Deleted:

Deleted: ...

Deleted: ...with head, thorax and 8 abdominal units; body body ... with oval pellets or scales, resembling calcium carbonate scales ... ; presence of such scales is a synapomorphy of ... Stratiomyidae+Xylomyidae ... (Figs. ... 2A-C, 3 A-C, 4 A-C, Supplementary figures 1, 2, 3, 4, 5, 6, 7). The The thorax of these specimens ... bears oval pellets or scales, rather than ... hardened sclerites as in Xylomyidae (Fig. ...)



Despite the overall similarity with larvae of Stratiomyidae, the fossil larvae of morphotype 1 exhibit several traits unknown among any modern forms of Stratiomyomorpha in general. 1) The head capsule of the fossil larvae is extremely elongated with tentorial arms and metacephalic rod reaching back up to the posterior edge of the prothorax (Fig. 3B). 2) The larvae possess long, triangular spines on the tergites of the trunk, as well as smaller rounded spines on the sternites of the trunk. This condition is unique among known larvae of Stratiomyomorpha, and probably represents an autapomorphy of the morphotype (Fig. 3C).

This new morphotype clearly differs from two other types of Stratiomyomorphan larvae recently reported from the Burmese amber (Liu et al. 2019), by the presence of the extremely long and strong spines on the trunk in the new form, as well as by the absence of the long setae on the posterior trunk (abdomen) and anterior trunk (thorax) (Figs. 2 A-C).

While the combination the features is, so far, unknown for Stratiomyomorpha, some of the characters are similar to the other Diptera larvae. Extremely elongated head capsules and large tergal spines are known in larvae of Asiloidea, especially in the groups Mydidae and Bombyliidae (Marshall, 2012). An elongated metacephalic rod is in particular common in larvae of Mydidae, Xylophagidae, Thervidae and Scenopidae (Hennig 1968, James 1981; Irwin and Leneborg 1981; Kelse 1981; Wilcox 1981). This makes the interpretation of morphotype 1 larvae relatively challenging, due to the "chimaera-like" combination of the traits, as a probable result of the "push of the past" effect (Baranov, Schädel, and Haug 2019; Haug and Haug 2019). This effect seems quite common among fossil representatives of Holometabola, representing phenomena occurring when initial diversification events in extant hyper diverse groups lead to a number of "experimental" morphologies (Budd and Mann 2018; Haug and Haug 2019). In total we have found 13 larvae of this morphotype, with seven of them being preserved in just two amber pieces (four in PED-0031 and three in PED-0152). Almost all larvae (except PED-0031\_1 and PED-0031\_2) show signs of severe, most probably pre-mortem damage, such as squashing, full-body piercing, and splitting the body medially (along the pleural region). In some cases, we even see complete mutilation with entire parts of the body (i.e. thorax) being absent from some specimens. The high abundance of this morphotype, as well as their high incidence of damage indicates that these larvae were both frequent, and probably a preferred prey to the other inhabitants of the amber forest in Myanmar. We discuss further aspects of the ecology further below.

**Morphotype 2:** This morphotype is featuring prominent oval pellets or scales, similar to calcium carbonate nodules of modern larvae of Stratiomyidae. Therefore, we consider this morphotype as a likely ingroup within Stratiomyidae (Figs. 5A-B, 6 A-D, Supplementary figure 9 A-B). A further interpretation within Stratiomyidae is more challenging, due to the relatively poor preservation. Yet, the absence of a coronet of so-called 'hydrofuge' setae on the terminal end and a relatively short body both point towards a terrestrial mode of life (McDfadden, 1967). Yet such autecological generalizations should be approached with caution. There are species with terrestrial larvae in groups that otherwise have mostly aquatic larvae (e.g. *Oxycera* (*Oxycera*) *leonina* (Panzer, 1798); Rozkošný 1987)). Also, the other way round, there are species with

**Deleted:** ... morphotype 1 exhibit ... several traits unknown among any modern forms of ... Stratiomyomorpha in general ... 1) The head capsule of the fossil larvae is extremely elongated with tentorial arms and metacephalic rod reaching back up to the posterior edge of the prothorax (Fig. ... 3B). 2) The larvae possess long, triangular spines on the tergites of of the trunk, as well as smaller rounded spines on the sternites of the trunk. This condition is unique among known larvae of Stratiomyomorpha, and probably represents an autapomorphy of the morphotype (Fig. ... )

**Deleted:** ... anterior trunk (thorax) (Figs. ... )

**Deleted:** ... for Stratiomyomorpha, some of the ... characters are similar to the other Diptera larvae. Extremely elongated head capsules and large tergal spines are known in larvae of Asiloidea, especially in the groups Mydidae and Bombyliidae ... (Marshall, 2012). An elongated metacephalic rod is in particular particular common in larvae of Mydidae, Xylophagidae, Thervidae and Scenopidae (Hennig 1968, James 1981; Irwin and Leneborg 1981; Kelse 1981; Wilcox 1981). This makes the interpretation of ... morphotype 1 larvae ... relatively challenging, due to the "chimaera-like" combination of the traits, as a probable result of the "push of the past" effect (Baranov, Schädel, and Haug 2019; Haug and Haug 2019). This effect seems quite common among fossil representatives of Holometabola, representing phenomena occurring when initial diversification events in ... extant ... hyper diverse groups leads... to a number of "experimental" morphologies (Budd and Mann 2018 ... ; Haug and Haug 2019). In total we have found 13 larvae of this ... )

**Deleted:** ... as a likely ingroup ... within Stratiomyidae (Figs. ... 5A-B, ... 6 A-D, Supplementary figure ... 9 A-B). A further interpretation within Stratiomyidae is more challenging, due to the relatively poor preservation. Yet, the absence of a coronet of so-called 'hydrofuge' setae on the terminal end and a relatively short body both point towards a terrestrial mode of life (McDfadden ... 1967). Yet such autecological generalizations should be approached with caution. There are species with terrestrial larvae in groups that otherwise have mostly aquatic larvae (e.g. *Oxycera* (*Oxycera*) *leonina* (Panzer, 1798); Rozkošný 1987)). Also...

aquatic larvae in groups that generally have terrestrial larvae (e.g. *Ptecticus*; Jung et al. 2012). Therefore, morphology of the fossil alone can be an indication, but never a proof of the autecological affinities of an animal.

Also, this new morphotype clearly differs from two other types of Stratiomyomorpha larvae recently described from amber from Myanmar (Liu, Hakim, and Huang 2020), by the much longer head capsule (in relation to the body), absence of the any spines on the tergites, as well as by the absence of long setae on the trunk.

**Deleted:** Also, this new morphotype clearly differs from two other types of Stratiomyomorpha larvae recently described from amber from Myanmar (Liu, Hakim, and Huang 2020), by the much longer head capsule (in relation to the body), absence of the any spines on the tergites, as well as by the absence of long setae on the trunk.

**Morphotype 3:** This morphotype clearly has closer relationships with Stratiomyidae based on the presence of a honeycomb pattern formed by oval pellets or scales, presence of a mandibular-maxillary complex and presence of brushes on this complex. Additionally, the habitus of the larva is highly reminiscent of extant terrestrial larvae of the group Stratiomyidae (see below).

Within Stratiomyidae, the specimen can be interpreted as an ingroup of Pachygastrinae based on the following combination of characters: absence of a coronet of so-called 'hydrofuge' on the trunk end; larva uniformly colored; trunk tergites with transversal rows of 6 setae each; labium not sclerotized and weakly developed; dorsal part of the mandibular-maxillary complex sclerotized; larva small larva, less than 10 mm (Rozkošný 1981, 1982). Within Pachygastrinae the specimen appears most similar to larvae of the group *Gowdeyana* Curran, 1928 in lacking cuticular "teeth" along the anal opening; thoracic leg group setae paired; all setae in the dorsal transversal row are subequal (Figs 7 A, B, 9).

**Deleted:** ... clearly has closer relationships with Stratiomyidae based on the presence of a honeycomb pattern formed by oval pellets or scales, presence of a mandibular-maxillary complex and presence of brushes on this complex. Additionally, the habitus of the larva is highly reminiscent of extant terrestrial larvae of the group Stratiomyidae (see below). Within Stratiomyidae, the specimen can be interpreted as an ingroup of Pachygastrinae based on the following combination of characters: absence of a coronet of so-called 'hydrofuge' on the trunk end; larva uniformly colored; trunk tergites with transversal rows of 6 setae each; labium not sclerotized and weakly developed; dorsal part of the mandibular-maxillary complex sclerotized; larva small larva, less than 10 mm (Rozkošný 1981, 1982). Within Pachygastrinae the specimen appears most similar to larvae of the group *Gowdeyana* Curran, 1928 in lacking cuticular "teeth" along the anal opening; thoracic leg group setae paired; all setae in the dorsal transversal row are subequal (Figs. ...).

In general, the larva is relatively unusual for Pachygastrinae, as it is larger than most last-stage Pachygastrinae larvae (9.5 mm vs 3–8 mm) and has a peculiar trunk end, elongated, ending with two large spines around the anus. It is possible that this larva belongs to an extinct lineage of Pachygastrinae, and large spines on the trunk and trunk end could represent an autapomorphy of this lineage. Yet, one should bear in mind that larvae for less than 10% of extant species Pachygastrinae are known (Bucánková, Kovac, and Rozkošný 2009). Hence the possibility remains that the larva may also belong to an extant ingroup of which the larvae are not yet known.

**Deleted:** ... unusual for Pachygastrinae, as it is larger than most last-stage Pachygastrinae larvae (9.5 mm vs 3–8 mm) and has a peculiar trunk end, elongated, ending with two large spines around the anus. It is possible that this larva belongs to an extinct lineage of Pachygastrinae, and large spines on the trunk and trunk end could represent an autapomorphy of this lineage. Yet, one should bear in mind that larvae for less than 10% of extant species Pachygastrinae are known (Bucánková, Kovac, and ...).

Currently there are two species of Pachygastrinae known as adults from Dominican and Mexican amber: *Pachygaster hymenaea* Grund & Hauser, 2005 (Supplementary figures 11 A, B) and *P. antiqua* James, 1971. The new fossil larva does not fit into the group *Pachygaster*, as in contrast to larvae of *Pachygaster*, the new larva does not have three setae in the "thoracic leg group" of setae. Also, the new larva is notably larger than any known larva of *Pachygaster* (Grund and Hauser 2005). It is important to note however, that the specimen is rather poorly preserved, and identification should be seen rather as approximation of the phylogenetic affinity rather than final conclusion.

**Deleted:**

**Morphotype 4:** This morphotype clearly has closer relationships with Stratiomyidae based on the presence of a honeycomb pattern formed by oval pellets or scales, presence of a mandibular-maxillary complex and presence of brushes on this complex. Additionally, the habitus of the larva is highly reminiscent of extant terrestrial larvae of the group Stratiomyidae

**Deleted:** ... clearly has closer relationships with Stratiomyidae based on the presence of a honeycomb pattern formed by oval pellets or scales, presence of a mandibular-maxillary complex ...

(see below). Within Stratiomyidae, further identification is impossible, due to the insufficient preservation of the specimen. The habitus in general, is reminiscent of terrestrial larvae of Stratiomyidae, i.e. from the ingroup Pachygastrinae (Rozkošný 1981).

Considering the exceptional preservation of this cuticle fossil, it is important to remember the possibility of contamination of the geological record by modern day holometabolan larvae, in particular fly larvae (Rasnitsyn 2008). Fly larvae are known to crawl into narrow fissures within shales and other types of rocks, effectively creating a hard to spot contamination in the fossil record. The specimen in question has its cuticle interlaced with numerous grains of the sedimentary matrix. In this aspect it is similar to the contamination of late Cretaceous sandstone by an extant fly *Protophormia terranova*, as reported by Rasnitsyn (2008: p. 249, figs. 96-97). Yet, the fossil in general seems not to be entirely dissimilar from other euarthropodan fossils known from the same formation, in terms of its preservation (Gašparič and Hyžný 2015).

Additionally, the specimen was collected from a fresh split rock sample and an imprint was observed on the negative (unfortunately not collected). Still, we cannot entirely rule out that this larva is an extant contamination of the shale (Gašparič and Hyžný 2015).

**Morphotype 5:** This morphotype seems to be a representative of Stratiomyidae, probably of the ingroups Stratiomyinae, Raphiocerinae or Nemotelinae, based on the presence of a coronet of hydrofuge setae (Rozkošný 1981; Pujol-luz et al 2004). The apical position of this coronet on the trunk end is not compatible with an interpretation as an ingroup of Nemotelinae (Hauser, Woodley, and Fachin 2017).

Not much more information could be gained from the larva, except that the hydrofuge setae coronet indicates an aquatic, rather than a terrestrial habitat of the animal (see discussion).

**Morphotype 6:** This morphotype is represented by two very poorly preserved fossils; therefore, no definitive statement on its phylogenetic affinity can be made. Nevertheless, we decided to include it here, due to the overall similarities in the body shape and presence of the coloration patterns of cuticle, like those in i.e. larvae of the group *Odontomyia* or other representatives of Stratiomyidae (Supplementary figure 14). For these reasons we think that it is prudent to consider this as a probable fossil of the Stratiomyidae, though there are no definite ways to further support this. This morphotype is too poorly preserved for any detailed systematic interpretation. Not much more information could be gained from the larvae, since the poorly preserved body falls into the "unknown" habitat category of the morphospace.

### The fossil record of Stratiomyidae

Given the important role of larval dipterans, their numerous ecosystem functions and their often very specific association with certain microhabitats (Baranov et al., 2019), their fossil records can provide a wealth of paleo-ecological information. Hence these new larval stratiomyomorph specimens widen our understanding of the respective paleo-ecosystems from which they originated. Even on the adult side" representatives of Stratiomyidae are rare in the fossil record, with only 73 occurrences (specimens) have been ever recorded (according to

Deleted: ...

Deleted: ... Considering the exceptional preservation of this cuticle fossil, it is important to remember the possibility of contamination of the geological record by modern day holometabolan larvae, in particular ... fly larvae (Rasnitsyn 2008 ...). Fly larvae are known to crawl into ...

Deleted: ... from a fresh split rock sample and an imprint was observed on the negative (unfortunately not collected). Still, we cannot entirely rule out that this ... larva is an extant contamination of the ...

Deleted:

Deleted: ... seems to ... be a representative of Stratiomyidae ... probably of the ingroups Stratiomyinae, Raphiocerinae or Nemotelinae, based on the presence of a coronet of hydrofuge setae ...

Deleted: ...

Deleted: ... Morphotype 6: This morphotype is represented by two very poorly preserved fossils; therefore, no definitive statement on its phylogenetic affinity can be made. Nevertheless, we decided to include it here, due to the overall similarities in the body shape and presence of the coloration patterns of cuticle, like those in i.e. larvae of the group *Odontomyia* or other representatives of Stratiomyidae (Supplementary figure 14). For these reasons we think that it is prudent to consider this as a probable fossil of the Stratiomyidae, though there are no definite ways to further support this. This morphotype is too poorly preserved for any detailed systematic interpretation. Not much more information could be gained from the larvae, since the poorly preserved body falls into the "unknown" habitat category ... of the morphospace 13 A) (Fig..

Deleted: ... Baranov et al., 2019), their fossil records can provide a wealth of ... paleo-ecological information. ... Hence these new larval stratiomyomorph specimens widen our understanding of the respective ... paleo-ecosystems from which they originated. Even on the adult side" representatives of Stratiomyidae are ...

PBDB, for the search parameters see Methods). This number is however excluding representatives of a unique, extinct group of flies with the long proboscides (Zhangsolvidae), known from the Early Cretaceous of China and Brazil, as well as Late Cretaceous of Myanmar (Peñalver et al. 2015). These flies have emerged as important pollinators of the gymnosperm plants in Cretaceous (Peñalver et al. 2015).

It is common for many organisms living in water to leave traces of their activity. Hence it should not be surprising that in the deep past ichnofossils provide most of the geological record of larval activity of Stratiomyidae, rather than body fossils. The most common example is the Jurassic "ichnogenus" *Helminthopsis* Heer 1877. It was interpreted as originally caused by larvae of soldier flies of the group *Stratiomys* Geoffroy, 1762 or at least a closely related species (Mángano, Buatois, and Claps 1996). This expands the potential range of the geological record of the group from the Barremian (Cretaceous) to the mid Jurassic (Mángano, Buatois, and Claps 1996; Pickerill, Han, and Jiang 1998). Body fossils of stratiomyomorphans, as mentioned, are rare. All known larval fossil records are listed in Table 1, together with the material used in this contribution. Myanmar amber seems to be particularly rich in stratiomyomorph larval, as the number of morphotypes known from this deposit now has reached four. Liu et al. (Liu, Hakim, and Huang 2020) have described two morphotypes of stratiomyomorph larval from this amber. Both morphotypes are characterized by features intermediate between two stratiomyomorph ingroups, Stratiomyidae and Xylomyidae (Liu, Hakim, and Huang 2020). Such chimera-like characteristics are also apparent in the one of the new morphotypes, namely morphotype 1. It can be interpreted as a result of the "Push of the past" phenomenon (Budd and Mann 2018). In contrast to morphotype 1, morphotype 2 from Myanmar amber has a much less conspicuous morphology, and seemingly is a representative Stratiomyidae s. str. as characterized by Hauser, Woodley, and Fachin (2017).

The record from Dominican amber, morphotype 3, is only the third record of the group Stratiomyomorpha from this otherwise very productive deposit (Grund and Hauser 2005). Only two specimens of the species *Pachygaster hymenea* Grund et Hauser, 2005 and a single specimen of *Nothomyia* sp. (Poinar and Poinar 1999) has so far been reported from Dominican amber. This could indicate that representatives of Stratiomyidae were either very rare in the Miocene of Hispaniola, or alternatively their autecology was precluding them from being preserved in amber (Solórzano Kraemer et al. 2018). The modern fauna of the isle of Hispaniola includes 13 species of Stratiomyidae (Perez-Gelabert 2008). This relationship of fossil specimens to extant species is quite different from the situation with another ingroup of Diptera, Chironomidae (non-biting midges). For Chironomidae, there are more fossil species known from Dominican amber, than there are extant species on the entire island of Hispaniola (Grund 2006). The situation of Chironomidae in Dominican amber can be explained by the fact that more attention was given to fossils of Chironomidae of Hispaniola, than to the extant ones. The same explanation cannot be applied to the discrepancy in species richness of fossil and extant species of Stratiomyidae. Soldier flies are mid-sized or even large flies; hence, they have a much lower chance of being overlooked in the amber records than Chironomidae. Modern

Deleted: ...

Deleted: ... Both ... morphotypes are characterized by features intermediate between ... two stratiomyomorph ingroups ... Stratiomyidae and Xylomyidae (Liu, Hakim, and Huang 2020). Such ... chimera-like characteristics are also apparent in the one of the new morphotypes, namely morphotype ... 1. It ... can be interpreted as a result of the "Push of the past" phenomenon (Budd and Mann 2018). In contrast ... to morphotype 1, morphotype 2 from Myanmar amber has a much less conspicuous morphology, and ... seemingly is a representative Stratiomyidae s. str. as ... characterized by ...

Deleted: ... from Dominican amber, ... morphotype morphotype 3, is only the third record of the group Stratiomyomorpha from this otherwise very productive deposit (Grund and Hauser 2005). Only ... two specimens of the species *Pachygaster hymenea* Grund et Hauser, 2005 and a single specimen of *Nothomyia* sp. (Poinar and Poinar 1999) has so far been reported from Dominican amber. This could indicate that representatives of Stratiomyidae were either very rare in the Miocene of Hispaniola, or alternatively their autecology was precluding them from being preserved in amber (Solórzano Kraemer et al. 2018). ... The modern fauna of the isle of Hispaniola includes 13 species of Stratiomyidae (Perez-Gelabert 2008). This relationship of fossil specimens to extant species is quite different from the situation with ... another ingroup of Diptera ... Chironomidae (non-biting midges). For Chironomidae ... there are more fossil species known from Dominican amber, than there are extant species on the entire island of Hispaniola (Grund 2006). ... The situation ... of Chironomidae in Dominican amber ... can be explained by the fact that more attention was given to fossils of Chironomidae of Hispaniola, than to the extant ones. The same explanation cannot be applied to the discrepancy in species richness of fossil and extant species of Stratiomyidae. Soldier flies are mid- ... sized or even large flies ... ; hence...

representatives of Stratiomyidae in the Neotropics and other tropical regions are associated with open areas in the forests or forest canopy (Woodley 2009; Hauser, Woodley, and Fachin 2017). We can therefore hypothesize that Dominican amber was capturing primarily animals associated with tree trunks, rather than canopy fauna or fauna of the open meadows within the forest. A similar capture pattern was shown for the Madagascar copal (Solórzano Kraemer et al. 2018).

The cuticle fossil from the Činžat (morphotype 4) originates from deep-water, low energy sedimentary environment (Gašparič and Hyžný 2015). It is difficult to explain how a larva of seemingly terrestrial Stratiomyidae ended up there. One possible explanation could be that the specimen drowned with driftwood and other terrestrial debris (which are present in the deposit) after a storm event.

Deleted:

The larva from Baltic amber is poorly preserved, and only identifiable as a larva of a soldier fly by the presence of the coronet of setae on the rear end. Overall, the fossil resembles extant aquatic larvae of the group *Odontomyia* (Supplementary figure 14 A, B), however, there are not enough diagnostic characters for a conclusive identification (also see discussion above). It is still conceivable that this specimen represents a species of Stratiomyidae with an aquatic larva. There are several larval forms of Insecta that have an aquatic lifestyle and have been recorded from Baltic amber. This includes immature of Odonata (damselflies), Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies) (Wichard, Gröhn, and Seredzsus 2009). Martinez-Delclòs, Briggs, and Peñalver (2004) suggested that aquatic larvae of Insecta can well be entrapped by still sticky resin pouring into water. This was probably the case for the larva from Baltic amber. This further supports that at least part of the Baltic amber deposits was formed directly next to water, probably in a swampy environment (Wichard, Gröhn, and Seredzsus 2009).

Deleted:

Deleted: OverallOverall, the fossil resembles extant aquatic ...  
...larvae of the group *Odontomyia* (Supplementary figure 14 A, B ...  
B ... ), however...however, there are not enough diagnostic  
characters for a conclusive identification (also see discussion above).  
It is still conceivable that this specimen represents a species of  
Stratiomyidae with an aquatic larva. There ... are several  
larval forms of Insecta that have an aquatic lifestyle and have been  
recorded from Baltic amber....This includes ... immature of  
Odonata (damselflies), Ephemeroptera (mayflies), Plecoptera  
(stoneflies) and Trichoptera (caddisflies) (Wichard, Gröhn, and  
Seredzsus 2009). ... Martinez-Delclòs, Briggs, and Peñalver  
(2004) suggested that aquatic ...

The possible record of larvae of Stratiomyinae from the Eocene of the former maar Lake Messel might represent a rare find of aquatic insect larvae from this deposit. Unfortunately, the larvae are too poorly preserved for the detailed interpretation. Aquatic insects are generally rare in the oil shale of Messel and in other maar lake deposits, because the fossil-bearing sediments (the so-called oil shale) formed only in the deeper parts of the former maar lake, not in its shore-region (Wedmann 2018). Aquatic insects, such as some larvae of Stratiomyidae were living in the shallow water in the shore region, and they could be only preserved as fossils when they drifted into the deeper, anoxic parts of the meromictic lake where the oil shale was formed.

Deleted: ... maar Lake Messel might ... represent a  
a rare find of aquatic insect larvae from this deposit. Unfortunately,  
the larvae are too poorly preserved for the detailed interpretation.  
Aquatic insects are generally rare in the ... oil shale of  
Messel and ... in other maar lake deposits ... , because  
the fossil-bearing sediments (the so-called ... oil shale)  
formed only in the deeper parts of the former maar lake, not in its  
shore-region (Wedmann 2018). Aquatic insects ... , such as  
some larvae of Stratiomyidae were living in the shallow water in the  
shore region, and they could be only preserved as fossils when they  
drifted into the deeper, anoxic parts of the meromictic lake where  
... the ...

#### Eco-morphological consideration

The ecomorphotype, or a shape of an organism adapted to a certain ecological condition, is used here as a proxy for the diversity of forms within a group of organisms. Outlines of the entire body, or parts of it have been shown as superior proxies for the shape of an organism in many

Deleted:



cases, when landmarks are hard to define, or when such landmarks do not reflect the shape of the organisms well enough (Tatsuta et al. 2018). One of the most often used methods for the outline capture in geometric morphometry is a Fourier Elliptical Transformation (Tatsuta, Takahashi, and Sakamaki 2018; Polášek et al. 2018). This method allows accessing the diversity of ecomorphotypes of a group of organisms by examining body outlines. Here we used all available fossil and extant Stratiomyomorpha larvae to trace the changes in the larval morphospace occupancy of the group and, consequentially indirectly, ecological diversity throughout its history.

**Deleted:** ... This method allows ... accessing the diversity of ecomorphotypes of a group of organisms by examining body outlines. Here we used all available fossil and extant ...

#### *Ecomorphology of extant stratiomyomorphan larvae*

New material examined in this study has shed a light on the far greater larval diversity of the group Stratiomyomorpha in deep time than was expected from the previously known geological records. We analyse the diversity of the ecological morphotypes of stratiomyomorphan larvae through time comparing it to modern ecomorphotype diversity. Here we use ecomorphotypes as a stable shape of an organism that evolved in response to certain ecological conditions (Rotheray 2019).

Stratiomyomorphan larvae are occupying three main types of habitats: 1) aquatic, 2) terrestrial, mostly upper soil, leaf litter, and lower vegetation, and 3) living wood, hence a saproxylic lifestyle. Many of the extant Stratiomyomorpha, in particular larvae of Pachygastrinae, are terrestrial saprotrophic and live under the bark of the dead wood (McFadden 1967; Marshall 2012).

**Deleted:** ... are occupying three main types of habitats: 1) aquatic, 2) terrestrial, mostly upper soil, leaf litter, and lower vegetation, and 3) living ... wood, hence a saproxylic lifestyle. Many of the extant Stratiomyomorpha, in particular larvae of Pachygastrinae, are ...

Larvae of Pantophthalmidae are saproxylic, inhabiting living wood (Marshall 2012). Many other larvae of Stratiomyidae (i.e. not those of Pachygastrinae), are occupying aquatic habitats. In the fossil record, we have some indisputably aquatic larvae, i.e. larvae *Odontomyia* sp. from Randecker Maar (Kühbänder and Schleich 1994) or larvae of *Stratiomyia* from the Holocene of Germany (Karl and Bellstedt 1989). The original habitats of other fossil larvae are less clear (Whalley and Jarzembowski 1985; Liu, Hakim, and Huang 2020).

**Deleted:** ... Pantophthalmidae are ... saproxylic, inhabiting living wood (Marshall 2012). Many other larvae of Stratiomyidae ... (i.e. not those of Pachygastrinae ...), are occupying aquatic habitats. ... In the fossil record, we have some indisputably aquatic larvae, i.e. larvae *Odontomyia* ... sp. from Randecker Maar (Kühbänder and Schleich 1994) or larvae of *Stratiomyia* from the Holocene of Germany (Karl and Bellstedt 1989). The original habitats of other fossil larvae ...

We have attempted to compare ecomorphotypes of the extant aquatic, terrestrial and saproxylic stratiomyomorphan larvae with the morphotypes of the fossil larvae. In doing so we hoped to elucidate the changes in the stratiomyomorphan larval morphospace through deep time, as a response to the changing environmental conditions. Our analysis has shown that stratiomyomorphan larvae are showing essentially four main morphotypes: 1) elongated aquatic larvae, roughly circular to oval in the cross-section, as larvae of *Stratiomyia*, *Oxycera*, *Odontomyia*, 2) terrestrial and saproxylic larvae with spindle-shaped or cylindrical bodies (Figs. 14A, B). Analyses of the shape distribution in morphospace have shown that thickness of the body and shape of the body at the ends are determining separation of the morphotypes. These two characteristics of shape are of the predominant importance, as they are making major contributions into the Principal components (P.C.) 1 and 2. These two P.C.s are explaining 36.1% and 21.2% of the shape variability respectively (Figs. 14A, B and Supplementary figure 15). It is important to note however, that no significant separation between the morphotypes

**Deleted:** ... , terrestrial and saproxylic stratiomyomorphan larvae with the morphotypes of the fossil larvae. In doing so we hoped to elucidate the changes in the stratiomyomorphan larval morphospace through deep time, as a response to the changing environmental conditions. ... Our analysis has shown that stratiomyomorphan larvae are showing essentially four main morphotypes: 1) elongated aquatic ... larvae, roughly circular to oval in the cross-section, as larvae of *Stratiomyia*, *Oxycera*, *Odontomyia*, 2) terrestrial and saproxylic larvae with spindle-shaped or cylindrical bodies (Figs. 143... B). Analyses of the shape distribution in morphospace have shown that thickness of the body and shape of the body at the ends are determining separation of the morphotypes. These two characteristics of shape are of the predominant importance, as they are making major contributions into the Principal components (P.C.) 1 and 2. These two P.C.s are explaining 36.1% and 21.2% of the shape variability respectively (Figs. 143...

exist, as ascertained by a MANOVA test. PC1 and PC2 components have  $p > 0.05$ , when the type of the habitat is used as an independent variable for morphotypes separation. This is also not surprising as "aquatic" and "terrestrial" groups of the larvae are overlapping broadly in the general shape, and the "saproxyllic" larvae morphotype is deeply nested in the "terrestrial" morphospace (Fig. 14A, B).

Deleted: 2

#### *Ecomorphology of fossil stratiomyomorphan larvae.*

The fossil larvae are widely distributed in the stratiomyomorphan morphospace (Figs. 14A, B). Most Cenozoic larvae (from Slovenian shale, Messel and Baltic amber) fall within the area occupied by modern forms. Also, some of the Cretaceous forms fall within the area occupied by modern forms.

Deleted: ... 143... B). Most Cenozoic larvae (from Slovenian ... shale, Messel and Baltic amber) fall within the area occupied by modern forms. Also, some of the Cretaceous forms fall within the area occupied by modern forms ...

Morphotypes 2, 3, 4 as well as the larvae from Liu et al. (2020) firmly fell into the part of the morphospace, occupied by modern terrestrial ecomorphotypes (Figs. 14A). The larva from Baltic amber plots into the "aquatic" type habitats, so did the specimens from morphotype 1, due to their elongated body (Fig. 14A). Despite that, we are hesitant to claim that morphotype 1 larvae are aquatic. Specimens of this morphotype are lacking the tell-tale characters of (most) extant aquatic stratiomyomorphan larvae, the coronet of 'hydrofuge' setae (Rozkošný 1991). Additionally, the extremely high abundance of morphotype 1 larvae (at least by the standards of the dipteran larvae in an amber deposit) can be explained by a possible close association with tree trunks. It is possible that these larvae lived under bark of trees, as seen in many extant larvae of Stratiomyidae (McFadden, 1967, Marshall, 2012). It is well known, that organisms associated with tree trunks in the amber forests, had higher chance of the preservation in amber (Solorzano-Kraemer et al 2018). On top of that, a rich set of the syninclusions present in the amber piece PED-0031 together with morphotype 1 larvae is pointing towards the terrestrial environment (Supplementary figures 2, 3). Such syninclusions include: a mite, a possible scale insect, parts of other representatives of Insecta, a fly of the group Bibionomorpha, a beetle larva, a spider and a millipede. This strongly indicates a terrestrial environment for morphotype 1 larvae.

Deleted: ... 3, 4 as well as the larvae from Liu et al. (2020) firmly fell into the part of the morphospace, occupied by ... modern terrestrial ecomorphotypes (Figs. ... 143...). The larva from Baltic amber ... plots into the "aquatic" type habitats, so did the specimens from morphotype 1, due to their elongated body (Fig. 143...). Despite that, we are hesitant to claim that morphotype 1 larvae are aquatic. Specimens of this morphotype are lacking the tell-tale characters of (most) extant aquatic stratiomyomorphan larvae, the coronet of 'hydrofuge' setae (Rozkošný 1991). Additionally, the extremely high abundance of morphotype 1 larvae (at least ... by the standards of the dipteran larvae in an amber deposit) can be explained by a possible close association with tree trunks ... It is possible that these larvae lived under ... bark of ... trees, as seen in many extant larvae of Stratiomyidae (McFadden, 1967, Marshall, 2012). ... It is well known, that organisms associated with tree trunks in the amber forests, had higher chance of the preservation in amber (Solorzano-Kraemer et al 2018). On top of that, a rich set of the syninclusions present in the amber piece PED-0031 together with morphotype 1 larvae is pointing towards the terrestrial environment (Supplementary figures 2, 3). Such syninclusions include: a mite, a possible scale insect, parts of other representatives of Insecta, a fly of the group Bibionomorpha, a beetle larva, a spider and a millipede. This strongly indicates a terrestrial environment for morphotype 1 larvae ...

Only one of the morphotypes described by Liu et al. (2019) falls outside of the morphospace occupied by the extant Stratiomyomorphan larvae (Fig. 14B, Supplementary figure 15).

Deleted: ... Only one of the morphotypes described by Liu et al. (2019) falls outside of the morphospace occupied by the extant Stratiomyomorphan larvae (Fig. 143...

Our analysis has shown that the morphospace of stratiomyomorphan larvae has become significantly larger over time. Only a small part of the occupied area of the morphospace was lost, when we are concerned with general body shape. We think that increase in the morphospace size of the Stratiomyomorpha can be explained by the gradual diversification of the group from the Late Cretaceous onwards as it was shown by Wiegmann et al. (2011).

Deleted: ... become significantly ... larger over time. Only a small part of the occupied area of the morphospace was lost, when we are concerned with general body shape ... We think that increase in the morphospace size of the Stratiomyomorpha can be explained by the gradual diversification of the group from the Late Cretaceous onwards as it was shown by Wiegmann et al. (2011). ...

#### Conclusions

The fossil record of dipteran larvae and pupae is generally skewed towards abundant forms from low-energy sedimentary basins, such as lake environments (Rasnitsyn and Quicke 2002). Therefore, groups with primarily aquatic immatures and high abundance, such as Chaoboridae and Chironomidae are over-represented in the fossil record (Rasnitsyn and Quicke 2002;

Zherikhin, Ponomarenko, and Rasnitsyn 2008). Aquatic larvae of other dipteran ingroups, while rare, have occasionally provided unprecedented insights into the evolution and palaeoecology of the group (Whalley and Jarzembowski 1985; Chen et al. 2014).

Terrestrial larvae of Diptera have been until recently considered extremely rare (Grimaldi and Engel 2005). Recent works, however, have shown that certain groups of terrestrial dipteran larvae can be quite abundant, at least in amber (Baranov, Schädel, and Haug 2019). Therefore, it is not entirely surprising to find new immature representatives of Stratiomyidae in Cretaceous, Neogenic and Paleogenic ambers, as well as in other types of fossil deposits. Further in-depth studies of amber and compression fossils collections will certainly lead to more new discoveries pertaining to larval biology of Stratiomyomorpha and other groups of Diptera.

### Acknowledgements

V.B. is grateful to M. Spies and D. Doczkal (ZSM Munich) for his invaluable help with collection of ZSM as well as help with the literature. We are grateful to Erica McAlister for her help with digitizing specimens from the London Natural History Museum. We are grateful to the editor and three anonymous reviewers for their efforts in improving this manuscript. Thanks to all people providing free software. We are grateful to Patrick Müller and Jonas Damzen for their invaluable support. J.M. Starck and Carolin Haug, both LMU Munich are thanked for long standing support.

Authors are grateful to Martin Hauser for his support and contribution to the manuscript improvement, as well as three anonymous reviewers and handling editor for their efforts to improve manuscript.

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:



## References

- Baranov, Viktor A., Mario Schädel, and Joachim T. Haug. 2019. "Fly Palaeo-Evo-Devo: Immature Stages of Bibionomorph Dipterans in Baltic and Bitterfeld Amber." *PeerJ* 7 (October): e7843. <https://doi.org/10.7717/peerj.7843>.
- Beuk, Paul. 1990 "Het voorkomen van *Zabrachia tenella* in Nederland (Diptera: Stratiomyidae)." *Entomologischen Berichten* 50: 101-106.
- Bonhomme, Vincent, Sandrine Picq, Cédric Gaucherel, and Julien Claude. 2014. "Momocs : Outline Analysis Using R." *Journal of Statistical Software* 56 (13): 1–24. <https://doi.org/10.18637/jss.v056.i13>.
- Bucánková, Alena, Damir Kovac, and Rudolf Rozkošný. 2009. "The Larva and Pupa of the Oriental *Pegadomyia pruinosa* Kertész, with a World List of the Described *Pachygastrinae* Larvae (Diptera: Stratiomyidae)." *Raffles Bulletin of Zoology* 57 (2): 239–49.
- Budd, Graham E., and Richard P. Mann. 2018. "History Is Written by the Victors: The Effect of the Push of the Past on the Fossil Record: PERSPECTIVE." *Evolution* 72 (11): 2276–91. <https://doi.org/10.1111/evo.13593>.
- Bull, R. M. 1976. "The Larval Stages of the Pasture and Yellow Soldier Flies, *Inopus rubriceps* (Macq.) and *I. flavus* (James) (Diptera, Stratiomyidae)." *Bulletin of Entomological Research* 65 (4): 567–72. <https://doi.org/10.1017/S0007485300006258>.
- Chen, Jun, Bo Wang, Michael S Engel, Torsten Wappler, Edmund A Jarzembowski, Haichun Zhang, Xiaoli Wang, Xiaoting Zheng, and Jes Rust. 2014. "Extreme Adaptations for Aquatic Ectoparasitism in a Jurassic Fly Larva." *ELife* 3 (June): e02844. <https://doi.org/10.7554/eLife.02844>.
- Cranston, Peter S., and Don R. Oliver. 1988. "Aquatic Xylophagous Orthoclaadiinae - Systematics and Ecology (Diptera, Chironomidae)." *Spixiana* 14: 143–54.
- Cruikshank, R.D., and Ko K. 2003. "Geology of an Amber Locality in the Hukawng Valley, Northern Myanmar." *Journal of Asian Earth Sciences* 21 (5): 441–55. [https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5).
- de Godoi, Fabio Siqueira Pitalug and Pujol-Luz, Jose Roberto. 2018 "Family Stratiomyidae" in Fusari, Livia Maria, Dantas, Galileu PS and Luiz Carlos Pinho (eds). "Order Diptera." In Thorp and Covich's Freshwater Invertebrates, pp. 771-778. Academic Press, 2018.
- Dubrovsky, A.Y. 2004. "New Data on *Pachygastrinae* (Diptera, Stratiomyidae) from Ukraine." *Vestnik Zoologii* 38 (6): 77–81.
- Dušek, Jindra and Rozkošný, Rudolf. 1967. "Revision mitteleuropäischer Arten der Familie Stratiomyidae (Diptera) mit besonderer Berücksichtigung der Fauna der ČSSR IV". *Acta Entomologica Bohemoslovaca* 64(2):140–165.
- Evenhuis, Neal L. Catalogue of the fossil flies of the world (Insecta: Diptera). Backhuys Publishers, 1994.
- Gašparič, Rok, and Matúš Hyžný. 2015. "An Early Miocene Deep-Water Decapod Crustacean Faunule from the Slovenian Part of the Styrian Basin, and Its Palaeoenvironmental and

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Palaeobiogeographical Significance." *Papers in Palaeontology* 1 (2): 141–66.  
<https://doi.org/10.1002/spp2.1006>.

Grimaldi, David A., and Michael S. Engel. 2005. *Evolution of the Insects*. Cambridge [U.K.]; New York: Cambridge University Press.

Grund, Martin. 2006. "Chironomidae (Diptera) in Dominican Amber as Indicators for Ecosystem Stability in the Caribbean." *Palaeogeography, Palaeoclimatology, Palaeoecology* 241 (3–4): 410–16. <https://doi.org/10.1016/j.palaeo.2006.04.005>.

Grund, Martin, and Martin Hauser. 2005. "Pachygaster Hymenaea Sp. Nov. and P. Antiqua James, 1971 (Diptera: Stratiomyidae) in Neotropical Ambers." *Zootaxa* 1061 (1): 29. <https://doi.org/10.11646/zootaxa.1061.1.2>.

Haug, Joachim T., and Carolin Haug. 2019. "Beetle Larvae with Unusually Large Terminal Ends and a Fossil That Beats Them All (Scraptiidae, Coleoptera)." *PeerJ* 7 (October): e7871. <https://doi.org/10.7717/peerj.7871>.

Haug, Joachim T, Carolin Haug, and Manfred Ehrlich. 2008. "First Fossil Stomatopod Larva (Arthropoda: Crustacea) and a New Way of Documenting Solnhofen Fossils (Upper Jurassic, Southern Germany)," 8.

Haug, Joachim T., Carolin Haug, Verena Kutschera, Gerd Mayer, Andreas Maas, Stefan Liebau, Christopher Castellani, Uwe Wolfram, Euan N. K. Clarkson, and Dieter Waloszek. 2011. "Autofluorescence Imaging, an Excellent Tool for Comparative Morphology: AUTOFLUORESCENCE IMAGING." *Journal of Microscopy* 244 (3): 259–72. <https://doi.org/10.1111/j.1365-2818.2011.03534.x>.

Haug, Joachim T., Carsten H. G. Müller, and Andy Sombke. 2013. "A Centipede Nymph in Baltic Amber and a New Approach to Document Amber Fossils." *Organisms Diversity & Evolution* 13 (3): 425–32. <https://doi.org/10.1007/s13127-013-0129-3>.

Hauser, Martin, Norman E. Woodley, and Diego A. Fachin. 2017. "Stratiomyidae (Soldier Flies)." In: Kirk-Spriggs, A.H. & Sinclair, B.J. (eds), *Manual of Afrotropical Diptera. Volume 2: Nematocerous Diptera and Lower Brachycera. Suricata 5*. Pretoria: South African National Biodiversity Institute. 919–79.

Hennig, Willi. 1952. "Die Larvenformen der Dipteren, Part III." Akademie Verlag, Berlin, 628 pp.

Iturralde-Vinent, Manuel A. 2001. "Geology of the Amber-Bearing Deposits of the Greater Antilles." *Caribbean Journal of Science* 37 (3): 141–67.

James, Maurice T. 1965. "Contributions to Our Knowledge of the Nearctic Pachygasterinae (Diptera: Stratiomyidae)." *Annals of the Entomological Society of America* 58 (6): 902–8. <https://doi.org/10.1093/aesa/58.6.902>.

———. 1981. "Stratiomyidae." In *Manual of Nearctic Diptera*, edited by J. F. McAlpine, B. W. Peterson, G. E. Shewell, H. J. Teskey, J. R. Vockeroth, and D. Monty Wood, 1:496–511. Agriculture Canada Monograph 27. Hull, Quebec, Canada: Canadian Government Publishing Centre.

**Deleted:** 633-640, edited by Art Borkent and Bradley J. Sinclair, 2:919–79. *Suricata 5*. Pretoria: South African National Biodiversity Institute. Hauser, Martin, Norman E. Woodley, and Diego A. Fachin. 2017. "Stratiomyidae (Soldier Flies)." In *Manual of Afrotropical Diptera. Volume 2: Nematocerous Diptera and Lower Brachycera*. Hauser, Martin, Norman E. Woodley,

**Deleted:** ¶  
¶

**Deleted:**

**Deleted:**

**Deleted:**

- Jelen, Bogomir, and Helena Rifelj. 2002. "Stratigraphic Structure of the B1 Tertiary Tectonostratigraphic Unit in Eastern Slovenia." *Geologija* 45 (1): 115–38. <https://doi.org/10.5474/geologija.2002.010>.
- Jung, Sang Woo, Bounthob Prayaysombath, Manichanh Nammanivong, Chanhvilay Somvongsa, and Yeon Jae Bae. 2012. "Aquatic insect fauna of Vang Vieng area in Northern Laos." *Entomological Research Bulletin* 28: 35–42.
- Karl, Hans-Volker, and Ronald Bellstedt. 1989. "Fossiler Rest einer Waffenfliegenlarve aus quartären Travertinbildungen Thüringens (Diptera, Stratiomyidae)." *Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologisches Museum und Institut für Spezielle Zoologie (Berlin)* 65 (2): 229–31. <https://doi.org/10.1002/mmzn.19890650205>.
- Krivoshchina, M. 2012. *Key to the Families and Genera of the Palearctic Dipterous Insects of the Suborder Nematocera, Based on Larvae [in Russian]*. Moscow: Publishing house KMK.
- Kühbander, M., and H. H. Schleich. 1994. "Odontomyia-Larven Aus Dem Randecker Maar (Insecta: Diptera, Stratiomyidae)." *Mitteilungen Der Bayerischen Staatssammlung Für Paläontologie Und Histor. Geologie* 34: 163–67.
- Lessard, Bryan D., David K. Yeates, and Norman E. Woodley. 2019. "Revision of the Hermetiinae of Australia (Diptera: Stratiomyidae)." *Austral Entomology* 58(1): 122–136.
- Liu, Yuming, Marina Hakim, and Diying Huang. 2020. "First Stratiomyomorph Larvae in the Mid-Cretaceous Amber from Myanmar (Diptera: Brachycera)." *Cretaceous Research* 106 (February): 104265. <https://doi.org/10.1016/j.cretres.2019.104265>.
- Mángano, M. Gabriela, Luis A. Buatois, and Guillermo L. Claps. 1996. "Grazing Trails Formed by Soldier Fly Larvae (Diptera: Stratiomyidae) and Their Paleoenvironmental and Paleocological Implications for the Fossil Record." *Ichnos* 4 (3): 163–67. <https://doi.org/10.1080/10420949609380124>.
- Marques, Karina I de S, and Roberto de Xerez. 2009. "Description of the Larva of Popanomyia Kerteszi James & Woodley (Diptera: Stratiomyidae) and Identification Key to Immature Stages of Pachygastrinae." *Neotropical Entomology* 38 (5): 643–48. <https://doi.org/10.1590/S1519-566X2009000500013>.
- Marshall, Stephen. 2012. *Flies. The Natural History and Diversity of Diptera*. Richmond Hill, Ontario: Firefly Press Ltd.
- Martínez-Delclòs, Xavier, Derek E.G Briggs, and Enrique Peñalver. 2004. "Taphonomy of Insects in Carbonates and Amber." *Palaeogeography, Palaeoclimatology, Palaeoecology* 203 (1–2): 19–64. [https://doi.org/10.1016/S0031-0182\(03\)00643-6](https://doi.org/10.1016/S0031-0182(03)00643-6).
- McFadden, Max W. 1967. "Soldier Fly Larvae in America North of Mexico." *Proceedings of the United States National Museum* 121 (3569): 1–72. <https://doi.org/10.5479/si.00963801.121-3569.1>.
- Mioč, P. 1972. *Tolmac Za List Slovenj Gradec. Osnovna Geološka Karta SFRJ 1:100,000*. Ljubljana, Slovenia: Zvezni geološki zavod.

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Mostovski, Mikhail B. 1998. "A brief review of brachycerous flies (Diptera, Brachycera) in the Mesozoic, with descriptions of some curious taxa." In *Proceedings of the First Palaeontomological Conference*, Moscow: 103-110.

Pape, Thomas, Vladimir Blagoderov, and Mikhail B. Mostovski. 2011. "Order Diptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.) *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness*." *Zootaxa* 3148 (1): 222. <https://doi.org/10.11646/zootaxa.3148.1.42>.

Peñalver, Enrique, Antonio Arillo, Ricardo Pérez-de la Fuente, Mark L. Riccio, Xavier Delclòs, Eduardo Barrón, and David A. Grimaldi. 2015. "Long-Proboscis Flies as Pollinators of Cretaceous Gymnosperms." *Current Biology* 25 (14): 1917–23. <https://doi.org/10.1016/j.cub.2015.05.062>.

Perez-Gelabert, Daniel E. 2008. "Arthropods of Hispaniola (Dominican Republic and Haiti): A Checklist and Bibliography." *Zootaxa* 1831 (1): 1–530. <https://doi.org/10.11646/zootaxa.1831.1.1>.

Pickerrill, Ron K., Yaojun Han, and Dazhi Jiang. 1998. "Taxonomic Review of the Ichnogenus Helminthopsis Heer 1877 with a Statistical Analysis of Selected Ichnospecies-a Reply." *Ichnos* 5 (4): 313–16. <https://doi.org/10.1080/10420949809386430>.

Poinar, George Jr., and Roberta Poinar. 1999. *The Amber Forest: A Reconstruction of a Vanished World*. Princeton, New Jersey: Princeton University Press.

Polášek, Marek, Roman J. Godunko, Sereina Rutschmann, Marek Svitok, Milan Novikmec, and Světlana Zahrádková. 2018. "Integrative Taxonomy of Genus Electrogena (Ephemeroptera: Heptageniidae): The Role of Innovative Morphological Analyses for Species Delimitation." *Arthropod Systematics & Phylogeny* 76 (3): 449–62.

Pujol-Luz, José Roberto, and Roberto De Xerez. 1999. "The Larva of Chalcidomorphina Aurata Enderlein 1914 (Diptera: Stratiomyidae) from 'Ilha de Marambaia,' Rio de Janeiro, Brazil." *Proceedings of the Entomological Society of Washington* 101 (2): 295–99.

Pujol-Luz, José Roberto, Roberto De Xerez and Viana, Gustavo Glória. 2004. "Descrição do pupário de Raphiocera armata (Wiedemann) (Diptera, Stratiomyidae) da Ilha da Marambaia, Rio de Janeiro, Brasil". *Revista Brasileira de Zoologia* 21 (4): 995–999.

Pujol-Luz JR, Pujol-Luz CVA 2014a. "Pantophthalmidae". In: Roig-Juñent S, Claps LE, Morrone JJ (Eds) Biodiversidad de Artrópodos Argentinos. Vol. 4. San Miguel de Tucumán, Editorial INSUE UNT, 391–397.

Pujol-Luz, José Roberto, Pujol-Luz, Cristiane V.A. 2014b. "Stratiomyidae". In: Roig-Juñent S, Claps LE, Morrone JJ (Eds) Biodiversidad de Artrópodos Argentinos. Vol. 4. San Miguel de Tucumán, Editorial INSUE UNT, 396–406.

Pujol-Luz, José Roberto, Welinton Ribamar Lopes, and Gustavo Glória Viana. 2016. "Description of the Puparium and Redescription of the Imagoes of Chorophthalmia Brevicornis Lindner (Diptera: Stratiomyidae)." *Zootaxa* 4121 (5): 583–88. <https://doi.org/10.11646/zootaxa.4121.5.8>.

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

R Core Team. 2014. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.

Rasnitsyn, Alexandr P. 2008. "Insects as contaminants of the fossil complexes [Nasekomye kak zagriazniteli iskopaemih kompleksov: In Russian]." In *Introduction into Palaeoentomology [Vvedeniye v Paleontologiyu: In Russian]*, edited by Vladimir V. Zherikhin, Alexandr G. Ponomarenko, and Alexandr P Rasnitsyn, 248–50. Moscow: Publishing house KMK.

Rasnitsyn, Alexandr P, and Donald L. J. Quicke, eds. 2002. *History of Insects*. New York, Boston, Dordrecht, London, Moscow: Kluwer Academic Publisher.

Rasser, M.W., Bechly, G., Böttcher, R., Ebner, M., Heizmann, E.P.J., Hölzke, O., Joachim, C., Kern, A.K., Kovar-Eder, J., Nebelsick, J.H. and Roth-Nebelsick, A. 2013. The Randeck Maar: Palaeoenvironment and habitat differentiation of a Miocene lacustrine system. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 392, 426-453.

Rotheray, Graham E. 2019. *Ecomorphology of Cyclorrhaphan Larvae (Diptera)*. Vol. 4. Zoological Monographs, Zoological Monographs. Cham, Switzerland: Springer International Publishing. <https://doi.org/10.1007/978-3-319-92546-2>.

Rozkošný, Rudolf. 1982. "A biosystematic study of the European Stratiomyidae (Diptera). Volume 1. Introduction, Beridinae, Sarginae, Stratiomyinae." A biosystematic study of the European Stratiomyidae (Diptera). Volume 1. Introduction, Beridinae, Sarginae, Stratiomyinae. Vol.1. Series Entomologica, Spencer, K.A.(ed.), Vol. 21, Springer Science & Business Media, Hague-Boston-London, 401pp.

Rozkošný, Rudolf. 1983. "A biosystematic Study of the European Stratiomyidae (Diptera): Volume 2-Clitellariinae, Hermediinae, Pachygasterinae and Bibliography". Vol.2. Series Entomologica, Spencer, K. A. (ed.), Vol. 25. Springer Science & Business Media, Hague-Boston-London, 431 pp.

Rozkošný, Rudolf, and Kovac, Damir. 1998. "Descriptions of Bamboo-Inhabiting Larvae and Puparia of Oriental Soldier Flies Ptecticus Brunettii and P. Flavifemoratus (Diptera: Stratiomyidae: Sarginae) with Observations on Their Biology." *European Journal of Entomology* 95: 65–86.

Rozkošný, Rudolf. 1997. "Diptera Stratiomyidae, Soldier Flies." In *Aquatic Insects of North Europe—A Taxonomic Handbook*, 2:321-332. Stenstrup: Appolo Books.

Schindelin, Johannes, Ignacio Arganda-Carreras, Erwin Frise, Verena Kaynig, Mark Longair, Tobias Pietzsch, Stephan Preibisch, Curtis Rueden, Stephan Saalfeld, Benjamin Schmid, Jean-Yves Tinevez, Daniel James White, Volker Hartenstein, Kevin Eliceiri, Pavel Tomancak & Albert Cardona 2012. "Fiji: An Open-Source Platform for Biological-Image Analysis." *Nature Methods* 9 (7): 676–82. <https://doi.org/10.1038/nmeth.2019>.

Schremmer, Fritz. 1951. "Die Mundteile der Brachycerenlarven und der Kopfbau der Larve von Stratiomys chamaeleon L.". *Österreichische Zoologische Zeitschrift* 3: 326–397.

Schremmer, Fritz. 1984. "Die polymetabole Larval-Entwicklung der Waffenfliegenart Hermetia illucens.—Ein Beitrag zur Metamorphose der Stratiomyidae)". *Annalen des Naturhistorischen Museums in Wien. Serie B für Botanik und Zoologie* 88/89: 405-429.

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted: <https://doi.org/10.1038/nmeth.2019>

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted: Schindelin, Johannes, Ignacio Arganda-Carreras, Erwin Frise, Verena Kaynig, Mark Longair, Tobias Pietzsch, Stephan Preibisch, Curtis Rueden, Stephan Saalfeld, Benjamin Schmid, Jean-Yves Tinevez, Daniel James White, Volker Hartenstein, Kevin Eliceiri, Pavel Tomancak and Albert Cardona et al. 2012. "Fiji: An Open-Source Platform for Biological-Image Analysis." *Nature Methods* 9 (7): 676–82....

Sinclair, Bradley.J. 1992. "A phylogenetic interpretation of the Brachycera (Diptera) based on the larval mandible and associated mouthpart structures". *Systematic Entomology* 17: 233-252.

Solórzano Kraemer, Mónica M., Xavier Delclòs, Matthew E. Clapham, Antonio Arillo, David Peris, Peter Jäger, Frauke Stebner, and Enrique Peñalver. 2018. "Arthropods in Modern Resins Reveal If Amber Accurately Recorded Forest Arthropod Communities." *Proceedings of the National Academy of Sciences* 115 (26): 6739–44. <https://doi.org/10.1073/pnas.1802138115>.

Stubbs, Alan E., and C. M. Drake. "British soldierflies and their allies: an illustrated guide to their identification and ecology: covering all flies (Diptera) in the families Acroceridae, Asilidae, Athericidae, Bombyliidae, Rhagionidae, Scenopinidae, Stratiomyidae, Tabanidae, Therevidae, Xylomyidae and Xylophagidae." British Entomological and Natural History Society, 2001.

Stuke, Jens-Hermann. 2003. "Die Stratiomyidae und Xylomyidae (Diptera) Niedersachsens und Bremens." *Braunschweiger Naturkundliche Schriften* 6(4): 831-856.

Tatsuta, Haruki, Kazuo H. Takahashi, and Yositaka Sakamaki. 2018. "Geometric Morphometrics in Entomology: Basics and Applications: Geometric Morphometrics in Entomology." *Entomological Science* 21 (2): 164–84. <https://doi.org/10.1111/ens.12293>.

Teskey, Herb.J, 1976. "Diptera Larva associated with trees in North America". *Memoirs of the Entomological Society of Canada* 100: 1-53.

Ulyshen, Michael D. 2018. "Saproxylic Diptera." In *Saproxylic Insects: Diversity, Ecology and Conservation*, edited by Michael D. Ulyshen, 1:167–92. Zoological Monographs 1. New York, NY: Springer International Publishing.

Wagner, Philipp, Joachim T. Haug, and Carolin Haug. 2019. "A New Calmanostracan Crustacean Species from the Cretaceous Yixian Formation and a Simple Approach for Differentiating Fossil Tadpole Shrimps and Their Relatives." *Zoological Letters* 5 (1): 20. <https://doi.org/10.1186/s40851-019-0136-0>.

Wedmann, Sonja. 2018. "Juwelen im Ölschiefer – Insekten und andere Wirbellose." In *Messel - Ein fossiles Tropenökosystem*, edited by Stephan F. K. Schaal, Krister T. Smith, and Jörg Habersetzer, 355. Senckenberg Bücher 79. Frankfurt am Main, Germany: Senckenberg.

Whalley, P.E.S., and E.A. Jarzembowski. 1985. "Fossil Insects from the Lithographic Limestone of Montsech (Late Jurassic-Early Cretaceous), Lérida Province, Spain." *Bulletin of the British Museum (Natural History)* 38 (5): 381–412.

Wichard, Wilfried, Carsten Gröhn, and Fabian Seredszus. 2009. *Aquatic Insects in Baltic Amber: Wasserinsekten Im Baltischen Bernstein*. Remagen-Oberwinter, Germany: Verlag Kessel.

Woodley, Norman E., and F. Christian Thompson. 2001 "A world catalog of the Stratiomyidae (Insecta: Diptera)"., *MYIA: The International Journal of the North American Dipterists' Society* 11:1-473.

Woodley, Norman E. 2009. "Stratiomyidae (Soldier Flies)." In *Manual of Central American Diptera*, edited by Brian V. Brown, 1:521–49. Ottawa, Ontario, Canada: NRC Research Press.

Xerez, Roberto de, and Emerson Garcia R. 2008. "Descrição Do Pupário de Chlamydonotum Nigreradiatum Lindner (Diptera: Stratiomyidae) Da Ilha Da Marambaia, Mangaratiba, RJ." *Neotropical Entomology* 37 (5): 567–70.

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Deleted:

Yu, Tingting, Richard Kelly, Lin Mu, Andrew Ross, Jim Kennedy, Pierre Broly, Fangyuan Xia, Haichun Zhang, Bo Wang, and David Dilcher. 2019. "An Ammonite Trapped in Burmese Amber." *Proceedings of the National Academy of Sciences* 116 (23): 11345–50. <https://doi.org/10.1073/pnas.1821292116>.

Zherikhin, Vladimir V., Alexandr G. Ponomarenko, and Alexandr P Rasnitsyn. 2008. *Introduction into Palaeoentomology [Vvedenije v Paleoentomologiju: In Russian]*. Moscow: Publishing house KMK.

|



Deleted:

Deleted:



## List of figures

Figure 1. Morphology of larva of the group Startiomyidae, exemplified by a larva of *Pachygaster atra*. A) Ventral view, marked; B) dorsal view, marked. Abbreviations: *a1-a7* – abdomen units one through seven, *ap* – anal setae, *asl* – anal slit, *as* – anterior spiracle, *D1-D3* – dorsal setae 1-3, *DL* – dorsolateral setae, *ep* – eye prominence, *hc* – head capsule, *L* – lateral setae (of abdomen unit), *L1-L2* – lateral setae (of trunk end), *mp* – maxillary palp, *mt* – metathorax, *pt* – prothorax, *sa* – subapical setae, *v1-v4* – ventral setae one – through four (of the trunk end), *V.L.* – ventrolateral setae (of the abdomen units 1-7).

Figure 2. Larva of morphotype 1, specimen PED-0031-2. A) Ventrolateral view; B) Ventrolateral view, marked; C) Dorsolateral view. Abbreviations: *hc* – head capsule, *as* – anterior spiracle; *pt* – prothorax, *mt* – metathorax, *a2-a6* – posterior trunk units 2-6, *te* – trunk end, *ps* – posterior spiracle.

Figure 3. Larva head of morphotype 1, specimen PED-0031-2. A) Lateral view; B) Lateral view, marked; C) Lateral view, line drawing. Abbreviations: *hs* – head soft tissues, *hc* – head capsule, *lb* – labrum; *la* – labium; *mk* – mandibular-maxillar complex, *ta* – tentorial arm, *mr* – metacephalic rode, *ct* – cut off through the part of the head capsule, *pt* – prothorax, *cc* – calcium carbonate pallet.

Figure 4. Larval head of morphotype 1, specimen PED-0152-2. A) Dorsal view, habitus; B) Ventral view, head; C) Ventral view, head, marked. Abbreviations: *mp* – maxillary palp, *bm* – base of mandibular-maxillar complex ("grinder"), *lb* – labrum.

Figure 5. Larva of morphotype 2, specimen LACM ENT 366281-1. A) Dorsal view, habitus; B) Dorsal view, habitus, marked. Ventral view, head; C) Ventral view, head, marked. Abbreviations: *hc* – head capsule, *as* – anterior spiracle; *ms* – mesothorax, *mt* – metathorax, *a1-a7* – posterior trunk units 1-7, *te* – trunk's end, *ps* – posterior spiracle.

Figure 6. Larval head of morphotype 2, specimens LACM ENT 366281-1(A-B) and LACM ENT 366281-2 (C-D). A) Dorsal view, head, LACM ENT 366281-1; B) Dorsal view, head - marked, LACM ENT 366281-1; C) Lateral view, head, LACM ENT 366281-2; D) Lateral view, head, marked, LACM ENT 366281-2. Abbreviations: *hs* – head soft tissues, *hc* – head capsule, *lb* – labrum; *mk* – mandibular-maxillar complex, *ey* – eyes; *as* – anterior spiracle.

Figure 7. Morphotype 3, habitus, ventral, larva PED-0462. A) Habitus, ventral view; B) Habitus, ventral view, marked. Abbreviations: *hc* – head capsule, *pt* – prothorax, *ms* – mesothorax, *mt* – metathorax, *a1-a7* – abdominal units 1-7, *te* – trunk end.

Deleted:

Deleted: ... Ventrolateral view; B) ... Ventrolateral view, marked; C) ... Dorsolateral view. Abbreviations: *hc* ... head capsule, *as* ... anterior spiracle; *pt* ... prothorax, *mt* ... metathorax, *a2-a6* ... posterior trunk units 2-6, *te* ... trunk end, *ps* ...

Deleted: ... Larva head of morphotype 1, specimen PED-0031-2. A) Lateral view; B) Lateral view, marked; C) Lateral view, line drawing. Abbreviations: *hs* ... head soft tissues, *hc* ... head capsule, *lb* ... labrum; *la* ... labium; *mk* ... mandibular-maxillar complex, *ta* ... tentorial arm, *mr* ... metacephalic rode, *ct* ... cut off through the part of the head capsule, *pt* ... prothorax, *cc* ...

Deleted: ... 4. Larval head of morphotype 1, specimen PED-0152-2. A) Dorsal view, habitus; B) Ventral view, head; C) Ventral view, head, marked. Abbreviations: *mp* ... maxillary palp, *bm* ... base of mandibular-maxillar complex ("grinder"), *lb* ...

Deleted: ... 5. Larva of morphotype 2, specimen LACM ENT 366281-1. A) Dorsal view, habitus; B) Dorsal view, habitus, marked. Ventral view, head; C) Ventral view, head, marked. Abbreviations: *hc* ... head capsule, *as* ... anterior spiracle; *ms* ... mesothorax, *mt* ... metathorax, *a1-a7* ... posterior trunk units 1-7, *te* ... trunk's end, *ps* ...

Deleted: ... 6. Larval head of morphotype 2, specimens LACM ENT 366281-1(A-B) and LACM ENT 366281-2 (C-D). A) Dorsal view, head, LACM ENT 366281-1; B) Dorsal view, head - marked, LACM ENT 366281-1; C) Lateral view, head, LACM ENT 366281-2; D) Lateral view, head, marked, LACM ENT 366281-2. Abbreviations: *hs* ... head soft tissues, *hc* ... head capsule, *lb* ... labrum; *mk* ... mandibular-maxillar complex, *ey* ... eyes; *as* ...

Deleted: ... 7. Morphotype 3, habitus, ventral, larva PED-0462. A) Habitus, ventral view; B) Habitus, ventral view, marked. Abbreviations: *hc* ... head capsule, *pt* ... prothorax, *ms* ... mesothorax, *mt* ... metathorax, *a1-a7* ... abdominal units 1-7, *te* ...

Deleted:

Figure 8. A-B) Fossil larvae of the group Pachygastrinae, morphotype 3, PED-0462 and C-D) head of larva of the extant species *Pachygaster atra*. A & B) Ventral view of the head capsule unmarked and marked; C & D) Ventral view of the head capsule unmarked and marked; Abbreviations: *an* – antennae; *as* – anal setae; *pt* – prothorax; *ey* – eyes; *lb* – labrum; *mp* – maxillar palp; *mb* – base of mandibular-maxillar complex ("grinder"); *v1-3* – ventral setae 1-3, *la* – labium.

**Deleted:** ... morphotype 3, PED-0462 and C-D) head of larva of the extant species *Pachygaster atra* ... A & B) Ventral view of the head capsule unmarked and marked; C & D) Ventral view of the head capsule unmarked and marked; Abbreviations: *an* – antennae; *as* – anal setae; *pt* – prothorax; *ey* – eyes; *lb* – labrum; *mp* – maxillar palp; *mb* – base of mandibular-maxillar complex ("grinder"); *v1-3* – ventral setae 1-3, *la* – labium.

Figure 9. Speculative reconstruction of the habitus and habitat of the fossil larva of the group Pachygastrinae, morphotype 3. *Onychophora Tertiapatus* sp stalking at the background. Artwork by Christian Mccal, reproduced with permission.

**Deleted:** e

Figure 10. Pachygastrinae, larva, morphotype 4, PED-0463. A) Habitus, ventral view; B) Habitus, ventral view, marked. Abbreviations: *hc* – head capsule; *ey* – eyes; *as* – anterior spiracle; *pt* – prothorax; *ms* – mesothorax; *mt* – metathorax; *a1-a7* – posterior trunk units 1-7, *te* – trunk end, *ps* – posterior spiracle, *fc* – folded cuticle.

**Deleted:** 9. Pachygastrinae, larva, morphotype 4, PED-0463 ... A) Habitus, ventral view; B) Habitus, ventral view, marked. Abbreviations: *hc* – head capsule; *ey* – eyes; *as* – anterior spiracle; *pt* – prothorax; *ms* – mesothorax; *mt* – metathorax; *a1-a7* – posterior trunk units 1-7, *te* – trunk end, *ps* – posterior spiracle, *fc* – folded cuticle.

Figure 11. Pachygastrinae, larva, morphotype 4, PED-0463, head ventrally. A) Head and prothorax, ventral view; B) Head and prothorax, ventral view, marked; C) Head, ventral view; D) Head, ventral view, marked. Abbreviations: *an* – antenna; *hc* – head capsule; *ey* – eyes; *as* – anterior spiracle; *lb* – labrum; *la* – labium; *mk* – mandibular-maxillar complex.

**Deleted:** 0. Pachygastrinae, larva, morphotype 4, PED-0463 ... head ventrally. A) Head and prothorax, ventral view; B) Head and prothorax, ventral view, marked; C) Head, ventral view; D) Head, ventral view, marked. Abbreviations: *an* – antenna; *hc* – head capsule; *ey* – eyes; *as* – anterior spiracle; *lb* – labrum; *la* – labium; *mk* – mandibular-maxillar complex.

Figure 12. Stratiomyinae, larva, morphotype 5 (PED-0464). A) Habitus; B) Close-up photo of coronet of the hydrofuge setae.

**Deleted:** 1. ...

Figure 13. Stratiomyinae, larvae, morphotype 6 (SF-MeI 4666). A) compression fossil, habitus; B) compression fossil, marked; C) overview. Abbreviations: *hc* – head capsule; *phc* – pharyngeal grinding mill; *pt* – prothorax; *mt* – metathorax; *a1-a6* – abdominal units; *te* – trunk's end.

**Deleted:** ... 132... Stratiomyinae, larvae, morphotype 6 (SF-MeI 4666). A) compression fossil, habitus; B) compression fossil, marked; C) overview. Abbreviations: *hc* – head capsule; *phc* – pharyngeal grinding mill; *pt* – prothorax; *mt* – metathorax; *a1-a6* – abdominal units; *te* – trunk's end.

Figure 14. Ecomorphospace occupied by extant and fossil larvae of the group Stratiomyomorpha. Both plots presenting the same morphospace, split by different grouping variables. Total captured variation = 57.3%; 36.1% at PC1 and 21.2% at PC2. A) Morphospace split by larval habitat: green – saproxylic, violet – terrestrial, blue – "unknown" (fossils), red – aquatic; B) Morphospace split by the geological age/deposit of the larvae: blue – extant, magenta – Myanmar amber, the rest of the deposits are represented by the single labelled dots.

**Deleted:** ... 143... Ecomorphospace occupied by extant and fossil larvae of the group Stratiomyomorpha. Both plots presenting the same morphospace, split by different grouping variables. Total captured variation = 57.3%; 36.1% at PC1 and 21.2% at PC2. A) Morphospace split by larval habitat: green – saproxylic, violet – terrestrial, blue – "unknown" (fossils), red – aquatic; B) Morphospace split by the geological age/deposit of the larvae: blue – extant, magenta – Myanmar amber, the rest of the deposits are represented by the single labelled dots.

