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

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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 extremely 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 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.

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26 **Abstract**
27 Stratiomyomorpha (soldier flies and allies) is an ingroup of Diptera, with a fossil record
28 stretching back to the Early Cretaceous (the Barremian, about 125 MYA). Stratiomyomorpha
29 includes at least 3000 species in the modern fauna, with many species being crucial for
30 ecosystem functions, especially as saprophages. Larvae of many stratiomyomorphans are
31 especially important as scavengers and saproxyls in modern ecosystems. Yet, fossil larvae of the
32 group are extremely scarce. Here we present 23 new records of fossil stratiomyomorphan larvae,
33 representing six discrete morphotypes. Specimens originate from Cretaceous amber from
34 Myanmar, Eocene Baltic amber, Miocene Dominican amber, and compression fossils from the
35 Eocene of Messel (Germany) and the Miocene of Slovenia. We discuss the implications of these
36 new records for our understanding of stratiomyomorphan ecomorphology in deep time as well as
37 their palaeoecology.
38
39 **Introduction**
40 Stratiomyomorpha is a group of flies (Diptera), which includes more than 3000 species of soldier
41 flies and allies in the modern -day fauna (Pape, Blagoderov, and Mostovski 2011). The major

42 ingroups of Stratiomyomorpha include: 1) Stratiomyidae, the group of true soldier flies, 2)
43 Xylomyidae, the group of wood soldier flies and 3) Pantophthalmidae, the group of giant timber
44 flies (Marshall 2012). The group Stratiomyomorpha has a fossil record reaching back about 125
45 million years into the past, to the Barremian (Lower Cretaceous; Whalley and Jarzembowski
46 1985; Mostovski 1998). A now-extinct group of flies with long proboscides (Zhangosolvidae)
47 from the Cretaceous has also been interpreted as an ingroup of Stratiomyomorpha (Peñalver et
48 al., 2015).
49   Representatives of Stratiomyomorpha are widespread in modern ecosystems and diverse
50 in their biology (Woodley, 2001; Marshall 2012). Larvae of different ingroups of
51 Stratiomyomorpha vary in habitat preferences. Fully aquatic larvae are known in Stratiomyinae ,
52 Rhaphiocerinae etc. (ingroups of Stratiomyidae); other larvae develop in the terrestrial habitats
53 as in the groups Pachygastrinae , Clitellariinae, Sargiinae or Hermetiinae (ingroups of
54 Stratiomyidae), and Xylomyidae , while larvae of timber flies (Pantophthalmidae) are
55 saproxylic, burrowing in living wood (James 1981, Rozkošný, 1981, 1982; Pujol-Luz. 2014).
56 Xylomyidae is a small group of lies with predacious or saprophagous larvae living under tree
57 bark (James 1981). Pantophthalmidae, the group of timber flies, including one of the largest
58 extant representatives of Diptera, with larvae burrowing in living wood (Rapp, 2007, 2011).
59   Representatives of Stratiomyomorpha are carrying vital ecosystem functions in their
60 respective habitats: 1) the larvae often act as important saprophages, involved in the cycling of
61 organic matter and 2) adults are important pollinators (Hauser, Woodley, and Fachin 2017).
62   One species of soldier flies, namely *Hermetia illucens* (Linnaeus,1758), with its fast -
63 growing scavenger-type larvae, is considered as an essential source of protein for feeding cattle
64 in industrial agriculture or for the production of human food (Hauser, Woodley, and Fachin
65 2017; Lessard et al. 2019). Many merolimnic species of Stratiomyomorpha, i.e. those with
66 aquatic larvae, are important algal mat grazers, involved in carbon cycling (Mángano, Buatois,
67 and Claps 1996).
68   Ichnofossils attributed to larvae of Stratiomyomorpha are quite common in the fossil
69 record (Mángano, Buatois, and Claps 1996; Pickerill, Han, and Jiang 1998), while body fossils
70 of this group have been scarce (Evenhuis 1994). So far,only five deposits are yielding any of
71 them:
72
73 1) Whalley & Jarzembowski (1985) reported four stratiomyomorphan larvae, differentiated into
74 two morphotypes, from the Early Cretaceous Montsech (Lerida, Spain, 125.45 to 122.46 Ma)
75 lithographic limestone of Spain.
76
77 2) Two morphotypes of larvae from Myanmar amber (~100 MYA) were reported by Liu et al.
78 (2019).
79

80   3) Kühbander & Schleich (1994) reported a stratiomyomorphan larva, interpreted as a larva of
81   the group *Odontomyia,* from the Miocene Randecker Maar in Germany (~17 MYA). Numerous
82   additional specimens were recorded later from the same deposit (Rasser et al., 2013).
83
84   4) Karl & Bellstedt (1989) reported a single body fossil of a larva of the group Stratiomyidae
85   from the Holocene of Eastern Germany (>1 MYA).
86
87   5) Sixteen fossil larvae of Stratiomyidae from the late Eocene of the Isle of Wight (129.4 ± 1.5
88   MYA) are present in the collection of the Natural History Museum London (UK). They can be
89   interpreted as aquatic forms of the group Stratiomyini and have been tentatively suggested to be
90   representatives of the species *Odontomyia brodiei* (Cockerell 1915) which is known from fossils
91   of adults from the same deposit (Krzeminski et al. 2019).
92   Larval forms are crucial for the success and diversification of any ingroup of
93   Holometabola, due to the ecological niche separation of the life stages (Grimaldi and Engel
94   2005). This applies to the super-diverse lineages of beetles (Coleoptera), wasps (Hymenoptera),
95   butterflies (Lepidoptera) and flies (Diptera), but also the less species-rich groups. Lack of fossil
96   larvae of Stratiomyomorpha is hampering progress in our understanding of the evolution of the
97   group. Here we report new records of larvae of Stratiomyomorpha based on new fossil
98   specimens. We furthermore discuss the ecological roles of the extinct larval forms based on
99   morphometric comparison of modern and fossil forms.
100
101
102 **Materials & Methods**
103
104 Material
105 Twenty-three specimens of fossil larvae are in the focus of this study. Twenty of them are
106 preserved in amber, and three are preserved as compression fossils. These larvae are representing
107 six morphotypes: two from Myanmar amber, one from Baltic amber, one from Dominican
108 amber, one from the Činžat shale of Slovenia, and the last one from the Messel lake deposits.
109 Most of the specimens in amber originated from Myanmar ("Burmese amber"), and most
110 represent a single morphotype ("morphotype 1"). Working with Burmese amber requires special
111 ethical consideration; for details, see the ongoing discussion (Haug et al., 2020). All these
112 specimens were purchased on ebay.com from different sellers and are now deposited at the
113 collection of the Palaeo-Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich,
114 Germany (PED) (PED -0152, PED-0349, PED-0362, PED-0031, PED-0041, PED-0243, PED-
115 0113, PED-0025). Specimens were purchased between the 20th of March and 1th of September
116 2019 from two ebay.com users. Details on the purchase of the every individual amber piece
117 (some containing multiple studied specimens) are available as ebay.com screenshtos in the
118 supplementary material.

119   A second morphotype (morphotype 2) also preserved in amber from Myanmar is
120   represented by five larval specimens, preserved in a single piece of amber (accession number
121   NHMLA-LACM ENT 366281). This specimen is deposited in the collection of the Los Angeles
122   County Museum of Natural History, Los Angeles, California, USA (LACM).
123   Specimen PED-0462, representing morphotype 3, was commercially acquired by Y.W.
124   and originated from the Dominican Republic. It is now deposited in the collection of the Palaeo-
125   Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany PED research
126   collections (PED).
127   Specimen PED-0463, representing morphotype 4, was collected by R.G. at the locality
128   Činžat, situated in the Ribnica-Selnica Graben, northern Slovenia. The specimen is now
129   deposited at the collection of the Palaeo-Evo-Devo Research Group, Ludwig-Maximilians-
130   Universität, Munich, Germany (PED).
131
132   Specimen PED-0464, representing morphotype 5, was obtained commercially from Mr.
133   Jonas Damzen (http://www.amberinclusions.eu) and stemmed from Yantarnyj, Kaliningrad
134   district (formerly Palmnicken, Königsberg). It is now deposited in the collection of the Palaeo-
135   Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany (PED).
136
137   Finally, two compression fossils originated from the Messel pit fossil site in Germany,
138   representing morphotype 6, are deposited under coll-no. SF-MeI 4666 in the collection of the
139   Forschungsinstitut und Naturmuseum Senckenberg (SF), Frankfurt-am-Main, Germany.
140   For comparative purposes, we used extant larval representatives of Stratiomyidae from
141   the collection of the Zoological State Collection, Munich (Zoologische Staatssammlung
142   München, ZSM), in particular larvae of: *Pachygaster atra* (Panzer, 1798), *Oxycera nigricornis*
143   Olivier, 1811, as well as *Odontomyia* sp. The latter is deposited in the collection of the Palaeo-
144   Evo-Devo Research Group, Ludwig-Maximilians-Universität, Munich, Germany (PED-0465).
145   For a full list of material please see Table 1.
146
147   Terminology: The morphological terminology mostly follows Rozkošný (1981, 1982) and
148   Sinclair (1992) for the head capsule morphology. Yet, to help non-experts, we amended some of
149   the special morphological terms with more general terms. As Insecta is an accepted ingroup of
150   Crustacea s.l. "crustacean"- structure names are given in brackets where necessary to provide
151   more comprehensive frame correspondence. It is important to note that many structures cannot
152   be discerned externally in the Diptera larvae, i.e. it is impossible to see any tergite boundaries in
153   the head capsule of the post-embryonic larvae. Nevertheless, it is well possible to reconstruct the
154   sequence of the segments in the head capsule, using the arrangement of the appendages (Baranov
155   et al., 2019).
156
157   Database use

158 Data on the fossil record of the group Stratiomyomorpha were downloaded from the
159 Paleobiology Database on 09 November 2019, using the group name "Stratiomyomorpha"
160 without any other filtering parameters.
161
162 Imaging methods
163 Amber specimens were imaged using a Keyence VHX-6000 Digital microscope, with ring-light
164 type illumination and/or cross-polarized, coaxial illumination. All images were recorded as
165 composite images to counteract the limitations of depth of the focus. Models were assembled
166 using stitching and panorama functions to overcome the weakness of the field of view under
167 higher magnifications. Each image detail was recorded by a stack of images of shifting focus to
168 overcome the limitation of the depth of field (Haug, Haug, and Ehrlich 2008; Haug et al. 2011;
169 Haug, Müller, and Sombke 2013). Fusion into sharp images and panorama stitching was
170 performed with the built-in software e.g., in Baranov, Schädel, and Haug (2019). We also
171 employed the built-in HDR function of the digital microscope; therefore, every single frame is a
172 composite from several images taken under different exposure times (cf. Haug et al. 2013).
173 Additionally, some specimens were imaged using a Keyence BZ-9000 fluorescence microscope
174 with either 2×, 4×, 10×or 20× objectives. Observations were conducted at an emitted wavelength
175 of 532 nm since it was the most compatible with the fluorescence capacities of the fossil
176 specimens (Haug et al. 2011). Also, here we recorded stacks of images which then were digitally
177 fused to single in-focus images using CombineZP (GNU). Compression fossils from Messel
178 were photographed with a Leica MZ12.5 stereomicroscope with an attached Nikon D300
179 camera.
180   The cuticle fossil, specimen PED-0463 ("morphotype 4"), was additionally imaged using
181 a scanning electron microscopy (SEM). Scanning was performed using a Carl Zeiss Leo 1430VP
182 scanning electron microscope in the Zoologische Staatssammlung München (Germany).
183 Scanning was performed with the beam current 80 μA; filament electric current 2500 A; and
184 electric potential 10-20 kV. Scanning was performed in a low vacuum (<2e-005 mbar).
185
186   Morphometry and outline analysis
187
188 The maximum dorsal head capsule length and width of some larvae were measured from the tip
189 of the labrum to the outer edge of the head capsule. Actual measurements were done from the
190 photos, using ImageJ, a public domain (Schindelin et al. 2012).
191   As a proxy for the overall shape diversity we compared the outlines of the larvae in the
192 dorsoventral aspect. To do so, we have analyzed the shapes, more precisely sketches of all
193 specimens, and extant comparative specimens with Fourier Elliptical Transformation using R
194 package Momocs (Bonhomme et al. 2014) and compared morphospace occupancy.
195   For the outline analysis we used black-and-white .jpg files, containing the outlines of all
196 available fossil stratiomyomorphan larvae as well as all extant stratiomyomorphan larvae for
197 which we were able to obtain a full-body image in the dorsoventral aspect from the literature.
198 Only specimens with a relatively straight body were included, as any examples imaged in curled

199 or bent position will heavily bias the morphospace. Full -body images of the larvae were
200 obtained from numerous published sources (Schremmer 1951; Hennig 1952; James 1965;
201 McFadden 1967; Bull 1976; Tuskey 1976; James 1981; Schremmer 1986; Beuk 1990; Rozkošný
202 1997; Rozkošný and Kovac 1998; Pujol-Luz and Xerez 1999; Stubbs and Darke 2001; Stuke
203 2003; Pujol-Luz, Xerez and Viana 2004; de Xerez and Garcia 2008; Bucánková, Kovac, and
204 Rozkošný 2009; Marques and de Xerez 2009; Marshall 2012; Pujol-Luz and Pujol-Luz 2014a &
205 b; Pujol-Luz, Lopes, and Viana 2016; Godoi and Pujol-Luz 2018), see Supplementary Table 1
206 for the full information. In total 69 stratiomyomorphan specimens were analyzed (see
207 supplemental Table 1, supplementary images).
208   Black-and white outlines were produced using a polygonal tool and mask functionality of
209 the program FIJI (Schindelin et al. 2012). Jpg outlines were analyzed in R using the *momocs*
210 package (Bonhomme et al. 2014), with the shapes being characterized by 36 harmonics. Source
211 code, list of the material used for the outline production and all the underlying data are available
212 as supplementary material (supplement 3). To estimate the habitat affinity of the fossil larvae, we
213 plotted them into a single morphospace with the extant larvae. For the latter, we demarcated
214 saproxylic, aquatic, and terrestrial habitats. Based on the position of the fossil larvae in this
215 morphospace, we have attempted to assess their habitat affinity. All data analyses were
216 conducted in R version 3.4.1 (2017-06-30) - "Single Candle" (R Core Team 2014).
217
218 Data availability
219 All the specimens used in the paper are deposited in public collections (see Table 1). All the
220 outline jpg images are provided in the supplementary materials to this paper, together with the R
221 code used to conduct the analysis.
222
223 Geological context
224
225 The geological context of Myanmar (Cruickshank and Ko 2003; Yu et al. 2019), Dominican
226 (Iturralde-Vinent 2001) and Baltic (Wichard, Gröhn, and Seredszus 2009) ambers, as well as
227 Messel shale (e.g. Büchel and Schaal 2018), has been explained in detail in various previous
228 works.
229
230 The Locality of Činžat is much less well known to the broader audience than the three above
231 mentioned, so we are discussing it in further detail. The studied locality Činžat is situated in the
232 Ribnica-Selnica graben (Jelen and Rifelj 2002) filled with sediments once deposited in the
233 Central Paratethys sea (Rögl, 1998), within the westernmost parts of the Styrian Basin,
234 approximately 15 km west of Maribor. Here, strata of the Ivnik Beds (Mioč 1972) are exposed in
235 a belt from Maribor, on the northern slopes of the igneous Pohorje pluton, towards the town of
236 Radlje.
237   Fossil bearing micaceous laminated siltstones cover older pre-Cenozoic rocks and
238 sequences of loosely bound conglomerates, alternating with sandstones and siltstones of the
239 Ivnik Beds. A late Burdigalian age (Miocene) coinciding with the 'Karpatian' stage of the

240 regional scale was identified based on a benthic foraminifera association and nannoplankton
241 sampling (Gašparič and Hyžný 2015).
242   The fossil fauna includes decapod crustaceans, bivalves, gastropods, and echinoids,
243 which are randomly distributed within the siltstone layers of the Činžat section, although
244 individual layers and variations in lithology are more likely to have macrofaunal fossil remains.
245 Interbedded layers of sandstones and conglomerates contain no macrofossils. The faunal
246 association suggests low energy deep-water depositional environment with epibathyal water
247 depth exceeding 125 m (Gašparič and Hyžný 2015).
248
249 **Results**
250 In total we can distinguish six different morphotypes among the studied fossil larvae.
251 Description, general notes: to provide the necessary background, we first give a generalized
252 description of the characteristics of larvae of Stratiomyidae (and to some extent
253 Stratiomyomorpha) segment by segment.
254
255 General shared appearance
256 Habitus. Small to medium-sized larva with slightly dorsoventrally flattened, spindle-shaped
257 body. The body is fully covered with oval pellets, supposedly of calcium carbonate composition
258 (although it is impossible to ascertain this aspect for the fossil forms) (Figs 1 A-B, 2 A-C, 3A-C,
259 4A).
260   Body length from 2 mm to slightly less than 20 mm. The body differentiated into
261 presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs 1A-B, 2 A-C, 4 A-
262 C). Anterior segments are forming a distinct head capsule.
263   The head capsule sclerotized anteriorly, posterior part (one third to one half) reduced to
264 several longitudinal structures, retracted into the anterior trunk (prothorax). The head capsule is
265 formed by an ocular segment plus five post-ocular segments.
266   Ocular segment recognizable by its appendage derivative, clypeo-labral complex. The
267 Clypeus (clypeal sclerite) is longer than it is wide. Labrum is roughly triangular, much longer
268 than wide, strongly sclerotized (Figs. 2A-C, 3B, C). The segment with small stemmata ("eye
269 prominences"), anteromedially.
270   Post-ocular segment 1, with a pair of antennae [antennulae in generalized terminology].
271 The antenna of Stratiomyomorpha larvae stout, comprising two elements, sitting in dorsoanterior
272 position, or more towards the center of the dorsal surface of the head capsule. In many fossil
273 specimens not preserved or not visible (Figs. 4B, C)
274   Post-ocular segment 2 (intercalary segment) without externally recognizable structures,
275 not identifiable in the post embryonic development of most Diptera larvae. It might be argued
276 that discussion of such seemingly absent structure in the description is unnecessary, or mixing
277 conjectures with observed structures. We will say, on the contrary: there is the knowledge and
278 hence expectation of the presence of this segment based on prior expirience. Yet, we do not see
279 it. In broader comparison, this is, in fact, informative and needs to be included in the taxa
280 description.

281   Post-ocular segments 3 and 4 were recognizable by their appendages: mandibles and
282   maxillae [maxillula in generalized terminology]. Mandibles and maxillae form a single
283   compound, the mandibular-maxillary complex (autapomorphy of Stratyomyomorpha),
284   comprising elements largely indistinguishable, apart from the distal parts of the maxillae
285   (maxillary palp). Maxillary palps quite stout, but prominent (Schremmer 1951, Rozkošný 1981).
286   The proximal portion of the mandibular-maxillary complex, fully sclerotized; with strong, multi-
287   branched setae on its dorsodistal surface, as well as laterally. Distal part or palp, conical, with
288   two elements (palpomeres). The apical part of the mandibular-maxillary complex bears an
289   arrangement of the setae ("brush") of varying complexity (autapomorphy of Stratyomyomorpha).
290   Basal part bearing a ventral "grinder", which is heavily sclerotized (Figs. 3A-C, 4B, C). On the
291   ventral side, the mandibular-maxillary complex forms ventral plates, occupying the ventral side
292   of the head capsule (Sinclair 1992).
293   Trunk (thorax + abdomen) with eleven visible units, interpreted as thee thorax segments,
294   seven abdominal segments and a trunk end (abdomen unit 8). Cuticle covered with round
295   deposits of calcium carbonate pellets, forming a honeycomb-like pattern (autapomorphy of
296   Stratyomyomorpha). Remark: It is difficult to ascertain that the cuticle of the fossils is indeed
297   covered in calcium carbonate pellets. It cannot be excluded that such cuticle scales are simple
298   chitin as in larvae of the Ephydridae or Oestridae (Marshall 2012).
299   Trunk units are without any parapods, creeping welts or protuberances. Different
300   arrangements of spiracles possible: 1) Trunk bears nine pairs of spiracles (openings of the
301   tracheal system): one pair of spiracles on thr prothorax, and eight pairs on the posterior trunk
302   (abdomen). This type of tracheal system is called peripneustic (Hennig, 1952). 2) most spiracles
303   reduced, amphipneustic (spiracles present on prothorax and trunk end) or 3) methapneustic
304   (spiracles on trunk end only) (McFadden 1967) (Figs 2A-C, Supplementary figures 4A-D).
305   The anterior trunk or thorax has three segments, pro-, meso- and methathorax. Armament
306   represented by the calcium carbonate pellets and large rhombic sclerites on the sternites,
307   occasionally with some modified, spike-like setae. Prothorax with 2–3 pairs of anterodorsal setae
308   (Rozkošný 1981).
309   Mesothorax and metathorax have numerous dorsal and ventral setae as well as multiple
310   pellets of calcium carbonate (Figs. 1A, B). All three units (= segments in this case) of the
311   anterior trunk (thorax) are having very uniform setation. Each of the thoracic segments bears
312   three pairs of dorsal setae (D1–D3), one pair of dorsolateral setae, and one pair of ventrolateral
313   setae. Additionally, each thoracic segment bears two pairs of ventral setae (Figs 1 A, B). The
314   inner pair of ventral setae simple; the outer pair contains several branched setae. The latter also is
315   known as a "thoracic leg group" setae (Rozkošný 1981).
316   Posterior trunk (abdomen) units 1–7 with setae arranged in a uniform pattern. This
317   pattern includes three pairs of dorsal setae, in addition to a single pair of dorsolateral and a pair
318   of ventrolateral setae on each of the abdominal units. Each of these units also bears one or two
319   pairs of lateral setae. These lateral setae can be quite prominent. Additionally, three (sometimes
320   four) pairs of ventral setae arranged in a transverse row on the sternites of abdominal units 1–7

321   (Rozkošný 1981). The trunk end (abdomen unit 8) bears two pairs of lateral setae, which are
322   often quite long. Additionally, the trunk end bears one pair of subapical setae, and one pair of
323   apical setae. The setae of both groups are usually relativley short. Dorsal setae are present but
324   rarely prominent on the trunk end. A large anal cleft (anus) present on the ventro-terminal part of
325   the trunk end. Around this cleft, the ventral seta arranged in five pairs, situated along and behind
326   the anal cleft (Fig. 1B) (Rozkošný 1981).
327
328   **Summary of main results**
329
330   In total, we can distinguish six different morphotypes among the studied fossil larvae.
331   Morphotype 1 (Stratiomyomorpha)
332
333
334   Material examined: 13 specimens (PED-0025, PED-0031_1, PED-0031_2, PED-0031_3, PED-
335   0031_4, PED-0041, PED-0113, PED-0152_1, PED-0152_2, PED-0152_3, PED-0243, PED-
336   0349, PED-0362) in 8 amber pieces (see Table 1, Supplementary fig. 1). Most of the
337   measurement were performed on the two best preserved specimens PED-0031_1 and PED-0041
338   (Figs. 2 A-C, 3 A-C, 4A-C, Supplementary figures 1,2, 3, 4, 5, 6, 7). Syninclusions: see Table 1.
339
340   Description:
341   Habitus. Medium-sized larva with slightly dorsoventrally flattened, spindle-shaped body,
342   fully covered with oval pellets or scales (Figs. 2 A-C, 4A).
343   Body length 2.3-1.1 mm (n=9). The body differentiated into presumably 20 segments,
344   ocular segment plus 19 post-ocular segments (Figs. 2 A-C, 4A). Anterior segments forming a
345   distinct head capsule.
346   The head capsule sclerotized anteriorly, and the posterior part is reduced to several
347   longitudinal structures (unpaired metacephalic rod, paired tentorial arms) retracted into the
348   anterior trunk (prothorax and mesothorax). Dimensions of head capsule (including metacephalic
349   rod and the tentorial arms protruding far back into the prothorax (Figs. 4A-C).
350   Ocular segment recognizable by its appendage derivative, clypeo-labrum complex.
351   Clypeus (clypeal sclerite) longer than wide. Labrum is roughly triangular, much longer than
352   wide, strongly sclerotized (Figs. 3A-C, 4B, C). Segment with small apparent stemmata,
353   posterolaterally.
354   Post-ocular segment 1 recognizable by its pair of appendages, antenna [antennula].
355   Antenna prominent, robust 25 µm long (n=1) (Figs. 4B, C)
356   Post-ocular segment 2 (intercalary segment) without externally recognizable structures.
357   Post-ocular segments 3 & 4 are recognizable by its pair of appendages, mandibular-
358   maxillary complex (Figs. 2A-C, 3A-C). The proximal part of fully sclerotized with strong, multi-
359   branched setae on the dorsodistal surface, as well as laterally. Distal part, palp, conical, with two
360   elements (palpomeres). Basal part of the complex bearing a large molar "grinder", which is

361   occupying the almost entire ventral side of the head capsule and heavily sclerotized (Figs. 2A-C,
362   3B, C).
363   Post-ocular segment 5 recognizable by its appendages, forming the labium, represented
364   by a fleshy lobe.
365   Trunk (thorax+abdomen) with 11 visible units, interpreted as three thorax segments,
366   seven abdomen segments and a trunk end (abdomen unit 8). The trunk is yellowish-brown,
367   except for the very first unit which is light-yellow. The cuticle is covered with oval pellets or
368   scales. Units of the posterior trunk do however bear complex armament on dorsal and ventral
369   sclerites (tergites and sternites; Figs. 1A-C).
370   Anterior trunk, thorax with three segments, pro-, meso- and metathorax.
371   The prothorax 450-770 μm long (n=2), without protrusions. Oval pellets or scales
372   represents armament, and large rhombic sclerite on the sternite, with two rows of small, flat
373   spikes arranged anteriorly on sternite. Distinct spiracle (anterior spiracle) on shallow depression
374   at the posterolateral part of the prothorax (Figs 1A-C).
375   Mesothorax yellowish-brown, 360-540 μm long (n=2). With two rows of triangular, flat
376   spines on the anterior edge of sternite. Numerous oval pellets or scales.
377   Metathorax yellowish-brown, 400-660 μm long (n=2), bears two rows of triangular, flat
378   spines on the anterior edge of sternite, as well as numerous oval pellets or scales.
379   Posterior trunk, abdomen with eight distinct units. Anterior seven representing proper
380   segments.
381   Abdomen unit 1 rectangular in dorsoventral plain, 440-760 μm long (n=2). Bearing
382   numerous oval pellets or scales, as well as two rows of the small triangular spikes on the anterior
383   edge of the sternite. Posterior edge of dorsal sclerite, tergite, with a row of 12 robust,
384   dorsoventrally triangular spines.
385   Abdomen units 2-7 rectangular (370-920 μm long). Bearing numerous oval pellets or
386   scales. Posterior edge of dorsal sclerites, tergites, each with a row of robust triangular spines, 10-
387   12 such spines on abdomen units 2-6, 7 on abdomen unit 7.
388   Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) roughly trapezoid
389   in the dorsoventral view, 620-750 μm long (n=2). With three pairs of small lateral setae, two
390   pairs of strong black setae on two mounds at the middle of the tergite; two pairs of strong needle-
391   like setae on two smaller mounds at the distal edge of on dorsal tergite (syn-tergite?). Tergite
392   also bears posterior spiracles in a transversal cleft, ventrally. Large, transversal anal cleft,
393   surrounded by an elevated oval sclerotized area, of a markedly darker color than the rest of the
394   cuticle visible at the trunk end.
395
396
397   Morphotype 2 (Stratiomyomorpha: Stratiomyidae)
398
399   Material examined: LACM ENT 366281(5 specimens in a single piece). Most measurements are
400   based on a single specimen, well preserved and visible in dorsal aspect. (Figs. 5A-B, 6 A-D,
401   Supplementary figure 8 A-B).

402   Syninclusions: NA

403

404   Description:

405   Habitus. Medium-sized larva with somewhat dorsoventrally flattened, spindle-shaped

406   body, covered with oval pellets of the calcium carbonate (Figs. 5 A-B).

407   Body covered by the white film, precluding observation of many fine details. Length 3.3-

408   3.7 mm (n=3). Body differentiated into presumably 20 segments, ocular segment plus 19 post-

409   ocular segments (Figs. 5 A-B, Supplementary figure 8 A, B). Anterior segments are forming a

410   distinct head capsule.

411   The head capsule sclerotized anteriorly, posterior part reduced to several longitudinal

412   structures (unpaired metacephalic rod, paired tentorial arms), retracted into prothorax.

413   Dimensions of head capsule: 480 µm long, 340 µm wide (n=1).

414   The surface of the head capsule is covered with pellets of calcium carbonate (Figs. 6 A-

415   D).

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

417   Clypeus (clypeal sclerite) fused with the frontal sclerite. Labrum roughly beak-like (100 µm

418   long, 70 µm wide), much longer than wide, strongly sclerotized (Figs. 6 A-D). A segment with

419   small apparent stemmata, anterolaterally.

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

421   apparent.

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

423   Post-ocular segments 3 & 4 are recognizable by their pairs of appendages forming a

424   mandibular-maxillary complex, (Figs. 6 A-D). Distal lobe brown in color, distal ends chisel-like.

425   Palp (distal part) not visible on any of the specimens available. (Figs. 5A-D).

426   Post-ocular segment 5 is not recognizable, its appendages, presumably forming the

427   labium, not visible in any of the specimens available (Figs. 6A-D).

428   Trunk (thorax+abdomen) with 11 visible units, interpreted as three thorax segments,

429   seven abdomen segments and trunk end (abdomen unit 8). Trunk is yellowish-brown, except for

430   the very first unit which is light-yellow. Cuticle is covered with round deposits of calcium

431   carbonate pellets. Trunk dorsoventrally flattened, spindle-shaped, total length 1.9-2.7 (n=3) mm

432   long; densely covered with oval pellets or scales (Figs. 5 A-B, Supplementary figure 8 A, B).

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

434   The Prothorax is ring-like, 240µm long, 630 µm wide (n=1), with ventral excision at

435   place of head capsule insertion. Small spiracles on posterolateral surface. Prothorax bears no

436   protrusions. Oval pellets or scales represent the armament. The anterior spiracle sits on a conical

437   protrusion, ca. 35 µm long, spiracle itself with a single longitudinal opening (Figs. 5 A-B,

438   Supplementary figure 8 A, B).

439   Mesothorax is 110 µm long, 780 µm wide (n=1), ring-shaped, with no visible protrusion,

440   bearing numerous oval pellets or scales.

441   Metathorax is 180 µm long, 820µm wide (n=1), ring-shaped, with one pair of the long,

442   wavy setae.

443   Posterior trunk, abdomen with eight distinct units. Anterior seven representing true
444 segments.
445   Abdomen units 1-7 are wider than long (200-260 μm long; 900-1000 μm wide). All units
446 are bearing several wavy lateral setae; unit 7 additionally bears two lateral wavy setae.
447   Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) roughly square
448 shaped in dorsal or ventral view (502 μm long, 525 μm wide); with two pairs of the large, wavy
449 setae. Anal cleft is sitting on large elevated mounds posteriorly on tergite (Figs. 5 A-B,
450 Supplementary figure 8 A, B).
451
452 Morphotype 3 (Stratiomyomorpha: Stratiomyidae)
453
454 Material examined: Piece of Dominican amber with a single fossil larva from the PED collection
455 (collection number PED-0001; Figs. 7 A-B, 8 A-D, 9, Supplementary figures 9 A-B, 10 A-B).
456 The larva is well preserved, anterior trunk obscured ventrally by a large air bubble. Head capsule
457 details inaccessible.
458 Description:
459 Habitus. Medium-sized larva with dorsoventrally flattened body, and triangular posterior end in
460 the dorsoventral plain) (Figs. 7 A-B, 8 A-B, 9). The body armored with the oval pellets or scales.
461 Total length 9.5 mm. Body differentiated into presumably 20 segments, ocular segment plus 19
462 post-ocular segments (Figs. 7 A-B). Anterior segments forming a distinct head capsule.
463   The head capsule partially sclerotized, longer than wide, posterior part of the head
464 capsule is retracted into the trunk. Dimensions of head capsule: 720 μm long, 550 μm. The
465 surface of the head capsule is covered with small cuticular scales with oval pellets or scales (Fig.
466 7A-B).
467   Ocular segment recognizable by its appendage derivative, clypeo- labral complex. With 2
468 pairs of setae, 2 labral setae and 2 frontoclypeal setae. Clypeus continuous with labrum, clypeus
469 narrow, labrum expanding distally (Figs. 8 A, C). Segment with pair of apparent stemmata
470 (larval eyes).
471   Post-ocular segment 1 is recognizable by its pair of appendages, antennae [antennula],
472 inserting ventrolaterally at the anterior end of the head capsule (Figs. 8 B). Antenna short,
473 consists of two elements.
474   Post-ocular segment 2 (intercalary segment) without externally recognizable structures.
475   Post-ocular segments 3 & 4 are recognizable by its pair of appendages, mandibular-
476 maxillary complex. Proximal part is heavily sclerotized, with basal plates. Main part of the lobe
477 hook-shaped, continuous, with appendages of the following post-ocular segment, integrated into
478 the mandibular-maxillary complex. The inner surface forms longitudinal striated "molar" area
479 (Figs. 8 A, B). Distal lobe is fleshy, with numerous maxillary setae (Figs. 8 A, B).
480   Post-ocular segment 5 recognizable by its appendages, forming the labium. Labium
481 bearing 3 pairs setae (2 ventral setae and 4 ventrolateral). Proximal part of a labium forms a
482 funnel connected to the oral cavity. Labium distally with 2 projections, probably palps. Labium
483 is highly modified, connected to cibarial (pharyngeal) skeleton of the head capsule (Fig. 8A, B).

484   Trunk (thorax+abdomen) has 11 visible units, interpreted as three thorax segments, seven
485   abdominal units and a trunk end (abdominal segment 8) (Figs. 7 A-B, 8 A-D, Supplementary
486   figures 9 A-B, 10 A-B). The trunk is spindle-shaped in a dorsoventral plain, parallel sided in the
487   middle region, triangular at the hind-end. All units are bearing oval pellets or scales and long
488   setae.
489   Anterior trunk (thorax) has three segments: pro-, meso- and metathorax. Thoracic "leg"
490   setae groups are seemingly with two setae in each group (Figs. 7 A-B, 9, Supplementary figures
491   9 A-B, 10 A-B).
492   Prothorax is 760 µm long. Prothorax with numerous setae: four antero-dorsal, six dorsal,
493   two dorsolateral, four lateral, two ventrolateral and six ventral (Figs. 7 A-B, Supplementary
494   figures 9 A-B, 10 A-B). Prothorax bears a pair of spiracles.
495   Mesothorax is 800 µm long, with numerous setae: six dorsal, two dorsolateral, four
496   lateral, two ventrolateral and six ventrals.
497   Metathorax is 500 µm long, with numerous setae: six dorsal, two dorsolateral,
498   four lateral, two ventrolateral and six ventral setae (Figs. 6 A-B, Supplementary figures 9 A-B,
499   10 A-B).
500   Posterior trunk (abdomen) has 8 apparent units flattened dorsoventrally, mostly oval in the dorsal
501   plain, with triangular posterior hind-end, (Figs. 7 A-B, 9). Abdomen units 1-7 are with numerous
502   setae: six dorsal setae, two dorsolateral setae, four lateral setae, two ventrolateral setae four
503   ventral, on each segment (Figs. 7 A-B, Supplementary figures 9 A-B, 10 A-B).
504   Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) is triangular in
505   general shape, dorsoventrally,it has well visible anus on the ventroterminal part. The trunk end
506   carries numerous setae: ventral setae pairs v1 through v4, two pairs of anal setae and 8
507   dorsolateral setae. The terminal end is elongated into the two rod-shaped protrusions, each
508   carrying anal setae. No cuticular "teeth" are present along the anal opening (Fig. 7 A, B).
509
510   Morphotype 4 (Stratiomyomorpha: Stratiomyidae)
511
512   Material examined: small slab of the Činžat shale with a cuticular fossil of a larva. Specimen
513   split in half along the medio-lateral surface of the sternites, so that tergites of the posterior trunk
514   (units 5–8) are folded upon the tergites of the more anterior ones (1–4). Coloration of specimen
515   very well preserved (Figs. 10 A-B, 11 A-D, Supplementary figure 12 A-B, 13 A-D).
516   Description:
517   Habitus. Medium-sized larva with dorsoventrally flattened body and rounded posterior
518   end. Body armored with oval pellets or scales. Total length 6.4 mm. Body differentiated into
519   presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 10 A-B). Anterior
520   segments forming a distinct head capsule.
521   Anterior body visible in ventral perspective only, of the posterior part of the body
522   similarly, only the dorsal region can be seen. The body with distinct sclerites ventrally on the
523   anterior trunk, as well as dorsally on posterior trunk, bearing distinctly "leopard" pattern of

524   coloration. This pattern consists from the dark-grey and brownish-yellow spots of the irregular
525   shape (Figs. 10 A-B, Supplementary figure 12 A-B).
526   The head capsule is sclerotized, much longer than wide, posterior part of the head capsule
527   is retracted into the trunk. Dimensions of head capsule: 1000 µm long, 250 µm wide (Figs. 11 A-
528   D, Supplementary figure 13 B).
529   Ocular segment is recognizable by its appendage derivative: clypeo- labral complex.
530   Clypeus continuous with labrum, narrow and blade-shaped (Figs. 11 A-D). The ocular segment
531   has apair of apparent hemispherical stemmata (larval eyes), at about its mid-length,
532   dorsolaterally. The segment surface bears multiple small setae.
533   Post-ocular segment 1 is recognizable by its pair of appendages, antennae [antennula].
534   Antenna inserted dorsolaterally at the distal end of the head capsule (Figs. 11 A-D,
535   Supplementary figure 13 B). Antenna short, with two elements.
536   Post-ocular segment 2 (intercalary segment) without externally recognizable structures.
537   Post-ocular segments 3 & 4 are recognizable by its pair of appendages, forming the
538   mandibular-maxillary complex. The complex with a proximal lobe, heavily sclerotized, with
539   basal plates. The main part of the basal plate is a lobe hook-shaped, continuous with appendages
540   of the following post-ocular segment. The inner surface forms longitudinal striated "molar" area
541   (Figs. 11 A-D, Supplementary figure 13 B). Distally, the complex has fleshy lobe with numerous
542   setae (Fig. 11 A).
543   Post-ocular segment 5 is recognizable by its pair of appendages, forming the labium.
544   Labium bears three pairs of setae (two ventral setae and four ventrolateral), on the ventral and
545   lateral surface respectively. Proximal part of the labium forms a three-pronged structure, adjacent
546   to the oral cavity (Figs. 10 A-D, Supplementary figure 13 B).
547
548   Trunk (thorax+abdomen) has 11 visible units, interpreted as three thorax segments, seven
549   abdomen segments and a trunk end (abdomen unit 8). Trunk bears two pairs of spiracles
550   (openings of the tracheal system) (Figs. 10 A-B, Supplementary figure 12 A-B, 13 A, B).
551   Anterior trunk (thorax) consists of three segments, pro-, meso- and metathorax. Tergites
552   and sternites are sclerotized, bearing oval pellets or scales.
553   Prothorax is 300 µm long. Prothorax bears a pair of large spiracles (100 µm in diameter
554   at the opening). Prothorax has several small setae on the dorsal surface (Figs. 10 A-B,
555   Supplementary figure 12 A-B, 13 A, B)).
556   Mesothorax is 300 µm long, ring-shaped, bearing no spiracles, with lighter area in the
557   center of the sternite (probably due to the sediment filling the depressions of the fossil).
558   Metathorax is 250 µm, ring-shaped, with the lighter area in the center of the sternite
559   (probably due to the sediment filling the depressions of the fossil).
560   Posterior trunk (abdomen) with 8 distinct units. Anterior seven units representing prpoper
561   segments. Posterior trunk mostly oval with rounded posterior hind-end (Figs. 10 A-B,
562   Supplementary figure 12 A-B, 13 A, B).
563   Abdomen units 1-7 are 320-610 µm long. Cuticle is split along the lateral side, medio-
564   laterally; therefore units 5-7 (and the trunk end) are folded over the ventral parts of the units 1-4.

565 This damage reveals the inner dorsal surface of the abdomen units 5-7 (and the trunk end) for
566 direct observation.
567   Trunk end (abdomen unit 8, undifferentiated abdomen segments 8-11?) semicircular in
568 general shape (dorsoventral view). The trunk end has an anus on ventroterminal part. No
569 cuticular "teeth" are present along anal opening (Figs. 10 A-B, Supplementary figure 13 C).
570
571
572 Morphotype 5 (Stratiomyomorpha: Stratiomyidae: Stratiomyinae)
573 Material examined: a single fossil larva in a piece of Baltic amber from the PED collection
574 (collection number PED-7568-100). The larva is poorly preserved, covered with air bubbles and
575 cracks in amber; only rear end of the trunk visible well enough to provide any distinguishable
576 features (Figs. 12 A-B). The piece of amber contains several syninclusions: non-biting midge
577 male (Diptera, Chironomidae); window-gnat (Diptera, Anisopodidae), two dark-winged fungus
578 gnats (Diptera, Sciaridae), large spider (Araneae).
579
580 Description:
581 Habitus. Medium-sized larva with spindle-shaped body in dorsoventral view, end of the trunk
582 has prominent coronet of large setae. The body mostly obscured by cracks and bubbles in the
583 amber; only rear end is clearly visible. Total length is 4.3 mm. Body differentiated into
584 presumably 20 segments, ocular segment plus 19 post-ocular segments (Figs. 12 A-B).
585   Trunk (thorax+abdomen) spindle-shaped, parallel sided, rounded at the hind-end in
586 dorsoventral view. Anterior part of the trunk entirely obscured by cracks. Subdivision of thr units
587 unclear. Posterior trunk has densely arranged strong setae. The trunk end (undifferentiated
588 abdominal segments 8-11?) rounded in general shape, carries strong coronet formed by 19
589 unbranched setae (Figs. 12 A-B). Additionally, the trunk end bears a pair of large spiracles,
590 surrounded by the coronet of setae and upper and lower sclerotized "lips".
591
592 Morphotype 6 (possibly Stratiomyomorpha: Stratiomyidae)
593 Material examined: two fossil larvae on one slab from the Grube Messel, stored in the S.F.
594 collection (collection number SF-MeI 4666; Figs. 13 A-C). The fossils are originating from the
595 Messel Formation. Specimen was collected in the year 1994 in grid square E8, 0.9m to 1.1m
596 below local stratigraphic marker horizon alpha. The larvae are poorly preserved, only traces of
597 the head capsules and the rest of the bodies can be seen; no traces of any setae are preserved;
598 nevertheless, both specimens show a well-preserved coloration pattern of the tergites.
599
600 Description:
601   Habitus. Medium-sized larva with spindle-shaped body. Accessible only in dorsal aspect.
602   Body length is 3.0 to 3.5 mm (n=2). Body differentiated into presumably 20 segments,
603 ocular segment plus 19 post-ocular segments (Figs. 13 A-C). Anterior segments forming a
604 distinct head capsule.

605   Head capsule is partially sclerotized, longer than wide, posterior part of the head capsule
606 retracted into the anterior trunk (prothorax). Head capsule visible only in vague outlines, with
607 several longitudinal structures (unpaired – metacephalic rod, paired – tentorial arms). These
608 structures are heavily sclerotized. Posterior part of the head capsules is more heavily sclerotized
609 (Figs. 13 A-C). Width of head capsule is ca. 270µm. Other units of the body are difficult to
610 measure due to the poorly visible borders between the segments.
611   Anterior segments not apparent, without prominent structures.
612   Post-ocular segment 5 is recognizable by an internally located pharyngeal grinding mill
613 (visible in both fossil specimens; Fig. 13 C).
614   Trunk (thorax+abdomen) spindle-shaped, parallel-sided, rounded at the hind-end. With
615 eleven units: three thorax segments, seven abdomen segments plus trunk end. Units of the trunk
616 are much wider than long. No setae preserved. No traces of spiracles or a distal coronet of setae
617 present (Fig. 13 C).
618 Anterior trunk, thorax, consisting of pro-, meso-, and metathorax.
619   Prothorax with general outlines visible. Prothorax is heavily sclerotized; posterior part of
620 the head capsule can be seen retracted into the prothorax (Fig. 13 A-C).
621   Mesothorax has two distinct pigment dots at the hind edge (Fig. 13 A, C).
622   Metathorax has no spiracles (Fig. 13 A-C).
623   Posterior trunk (abdomen) with 8 units (Fig. 13 A-C).
624   Abdomen units 1-6 are bearing distinct lines of pigmentation, two medially on all
625 tergites, and two laterally on most tergites (Fig. 13 A-C).
626   Abdomen unit 7 hasno details preserved; only general outlines can be seen (Fig. 13 A-C).
627 Trunk end (Abdominal unit 8) with only general outline can be seen: the trunk endsquare in
628 general shape, with a rounded posterior edge, when viewed in the dorsoventral view (Fig. 13 A-
629 B). No spiracles or anus can be discerned.
630
631 **Discussion**
632
633 Systematic interpretation
634 All specimens can easily be identified as larval forms of Diptera. This interpretation can be based
635 on the general body shape of the specimen, the absence of walking ("ambulatory") legs on the
636 thorax, as well as the spiracle arrangement. The six morphotypes differ in numerous characters;
637 their systematic relationships are discussed.
638
639 *Morphotype 1*: This morphotype is interpreted to be a representative of the group soldier and
640 timber flies (Stratiomyomorpha) based on the following combination of characters (see Figs. 1
641 A-C, 2 A-C, 3 A-C, Supplementary figures 1,2, 3, 4, 5, 6, 7): larva elongated and flattened, with
642 head, thorax and 8 abdominal units; body with oval pellets or scales, resembling calcium
643 carbonate scales ; presence of such scales is a synapomorphy of Stratiomyidae+Xylomyidae .
644 (Figs. 2 A-C, 3 A-C, 4 A-C, Supplementary figures 1, 2, 3, 4, 5, 6, 7). The thorax of these
645 specimens bears oval pellets or scales, rather than hardened sclerites as in Xylomyidae (Fig. 2

646   B). Mandibles and maxillae are conjoined into a mandibular-maxillary complex (Fig, 4 B, C).
647   Larvae possess a large molar grinder and a setal brush at this mandibular-maxillary complex
648   (Figs. 4 B, C). The brush of the mandibular-maxillary complex, as indeed complex itself, is
649   substantially reduced and simplified (Figs. 4 B, C). This condition is, however, not uncommon
650   among extant representatives of Stratiomyidae, for example in mature larvae of Hermeteiinae
651   and Sarginae (Rozkošný 1981).
652   Despite the overall similarity with larvae of Stratiomyidae, the fossil larvae of
653   morphotype 1 exhibit several traits unknown among any modern forms of Stratiomyomorpha in
654   general. 1) The head capsule of the fossil larvae is extremely elongated with tentorial arms and
655   metacephalic rod reaching back up to the posterior edge of the prothorax (Fig. 3 B). 2) The
656   larvae possess long triangular spines on the tergites of the trunk, as well as smaller rounded
657   spines on the sternites of the trunk. This condition is unique among known larvae of
658   Stratiomyomorpha and probably represents an autapomorphy of the morphotype (Fig. 3C).
659   This new morphotype clearly differs from two other types of Stratiomyomorphan larvae
660   recently reported from the Burmese amber (Liu et al. 2019) by the presence of the extremely
661   long and strong spines on the trunk in the new form, as well as by the absence of the long setae
662   on the posterior trunk (abdomen) and anterior trunk (thorax) (Figs. 2 A-C).
663   While the combination the features is, so far, unknown for Stratiomyomorpha; some of
664   the characters are similar to the other Diptera larvae. Extremely elongated head capsules and
665   large tergal spines are known in larvae of Asiloidea, especially in the groups Mydidae and
666   Bombyliidae (Marshall, 2012). An elongated metacephalic rod is in particular common in larvae
667   of Mydidae, Xylophagidae, Thervidae and Scenopidae (Hennig 1968, James 1981; Irwin and
668   Leneborg 1981; Kelse 1981; Wilcox 1981). This makes the interpretation of morphotype 1 larvae
669   relatively challenging, due to the "chimaera-like" combination of the traits, as a probable result
670   of the "push of the past" effect (Baranov, Schädel, and Haug 2019; Haug and Haug 2019). This
671   effect seems quite common among fossil representatives of Holometabola, representing
672   phenomena occurring when initial diversification events in extant hyper diverse groups lead to a
673   number of "experimental" morphologies (Budd and Mann 2018; Haug and Haug 2019). In total
674   we have found 13 larvae of this morphotype, with seven of them being preserved in just two
675   amber pieces (four in PED-0031 and three in PED-0152). Almost all larvae (except PED-0031_1
676   and PED-0031_2) show signs of severe, most probably pre-mortem damage, such as squashing,
677   full-body piercing, and splitting the body medially (along the pleural region). In some cases, we
678   even see complete mutilation with entire parts of the body (i.e. thorax) being absent from some
679   specimens. The high abundance of this morphotype, as well as their high incidence of damage
680   indicates that these larvae were both frequent, and probably a preferred prey to the other
681   inhabitants of the amber forest in Myanmar. We discuss further aspects of the ecology further
682   below.
683
684   *Morphotype 2:* This morphotype is featuring prominent oval pellets or scales, similar to calcium
685   carbonate nodules of modern larvae of Stratiomyidae. Therefore, we consider this morphotype as
686   a likely ingroup within Stratiomyidae (Figs. 5 A-B, 6 A-D, Supplementary figure 9 A-B). A

687 further interpretation within Stratiomyidae is more challenging, due to the relatively poor
688 preservation. Yet, the absence of a coronet of so-called "hydrofuge" setae on the terminal end
689 and a relatively short body both point towards a terrestrial mode of life (McDFadden 1967). Yet
690 such autecological generalizations should be approached with caution. There are species with
691 terrestrial larvae in groups that otherwise have mostly aquatic larvae (e.g. *Oxycera* (*Oxycera*)
692 *leonina* (Panzer, 1798); Rozkošný 1987)). Also, the other way round, there are species with
693 aquatic larvae in groups that generally have terrestrial larvae (e.g. *Ptecticus*; Jung et al. 2012).
694 Therefore, morphology of the fossil alone can be an indication, but never a proof of the
695 autecological affinities of an animal.
696   Also, this new morphotype clearly differs from two other types of Stratiomyomorphans
697 larvae recently described from amber from Myanmar (Liu, Hakim, and Huang 2020), by the
698 much longer head capsule (in relation to the body), absence of the any spines on the tergites, as
699 well as by the absence of long setae on the trunk.
700
701 *Morphotype 3:* This morphotype clearly has closer relationships with Stratiomyidae based on the
702 presence of a honeycomb pattern formed by oval pellets or scales, presence of a mandibular-
703 maxillary complex and presence of brushes on this complex. Additionally, the habitus of the
704 larva is highly reminiscent of extant terrestrial larvae of the group Stratiomyidae (see below).
705   Within Stratiomyidae, the specimen can be interpreted as an ingroup of Pachygastrinae
706 based on the following combination of characters: absence of a coronet of so-called 'hydrofuge'
707 setae on the trunk end; larva uniformly colored; trunk tergites with transversal rows of 6 setae
708 each; labium not sclerotized and weakly developed; dorsal part of the mandibular-maxillary
709 complex sclerotized; small larva , less than 10 mm (Rozkošný 1981, 1982). Within
710 Pachygastrinae the specimen appears most similar to larvae of the group *Gowdeyana* Curran,
711 1928 in lacking cuticular "teeth" along the anal opening; thoracic leg group setae paired; all setae
712 in the dorsal transversal row are subequal (Figs. 7 A, B, 9).
713   In general, the larva is relatively unusual for Pachygastrinae, as it is larger than most last-
714 stage Pachygastrinae larvae (9.5 mm vs. 3 –8 mm) and has a peculiar trunk end, elongated,
715 ending with two large spines around the anus. It is possible that this larva belongs to an extinct
716 lineage of Pachygastrinae, and large spines on the trunk and trunk end could represent an
717 autapomorphy of this lineage. Yet, one should bear in mind that larvae for less than 10% of
718 extant species Pachygastrinae are known (Bucánková, Kovac, and Rozkošný 2009). Hence the
719 possibility remains that the larva may also belong to an extant ingroup of which the larvae are
720 not yet known.
721   Currently there are two species of Pachygastrinae known as adults from Dominican and
722 Mexican amber: *Pachygaster hymenaea* Grund & Hauser, 2005 (Supplementary figures 11 A, B)
723 and *P. antiqua* James, 1971. The new fossil larva does not fit into the group *Pachygaster,* as in
724 contrast to larvae of *Pachygaster*, the new larva does not have three setae in the "thoracic leg
725 group" of setae. Also, the new larva is notably larger than any known larva of *Pachygaster*
726 (Grund and Hauser 2005). It is important to note however, that the specimen is rather poorly

727   preserved, and identification should be seen rather as approximation of the phylogenetic affinity
728   rather than final conclusion.
729
730   *Morphotype 4:* This morphotype clearly has closer relationships with Stratiomyidae based on the
731   presence of a honeycomb pattern formed by oval pellets or scales, presence of a mandibular-
732   maxillary complex and presence of brushes on this complex. Additionally, the habitus of the
733   larva is highly reminiscent of extant terrestrial larvae of the group Stratiomyidae (see below).
734   Within Stratiomyidae, further identification is impossible, due to the insufficient preservation of
735   the specimen. The habitus in general, is reminiscent of terrestrial larvae of Stratiomyidae, i.e.
736   from the ingroup Pachygastrinae (Rozkošný 1981).
737   Considering the exceptional preservation of this cuticle fossil, it is important to remember
738   the possibility of contamination of the geological record by modern day holometabolan larvae, in
739   particular fly larvae (Rasnitsyn 2008). Fly larvae are known to crawl into narrow fissures within
740   shales and other types of rocks, effectively creating a hard to spot contamination in the fossil
741   record. The specimen in question has its cuticle interlaced with numerous grains of the
742   sedimentary matrix. In this aspect it is similar to the contamination of late Cretaceous sandstone
743   by an extant fly *Protophormia terranovae,* as reported by Rasnitsyn (2008: p. 249, figs. 96-97).
744   Yet, the fossil in general seems not to be entirely dissimilar from other euarthropodan
745   fossils known from the same formation, in terms of its preservation (Gašparič and Hyžný 2015).
746   Additionally, the specimen was collected from a fresh split rock sample and an imprint was
747   observed on the negative (unfortunately not collected). Still, we cannot entirely rule out that this
748   larva is an extant contamination of the shale (Gašparič and Hyžný 2015).
749
750   *Morphotype 5:* This morphotype seems to be a representative of Stratiomyidae , probably of the
751   ingroups Stratiomyinae, Raphiocerinae or Nemotelinae, based on the presence of a coronet of
752   "hydrofuge "setae (Rozkošný 1981; Pujol-luz et al 2004). The apical position of this coronet on
753   the trunk end is not compatible with an interpretation as an ingroup of Nemotelinae (Hauser,
754   Woodley, and Fachin 2017).
755   Not much more information could be gained from the larva, except that the
756   "hydrofuge"setae coronet indicates an aquatic, rather than a terrestrial habitat of the animal (see
757   discussion).
758
759   *Morphotype 6:* This morphotype is represented by two very poorly preserved fossils; therefore,
760   no definitive statement on its phylogenetic affinity can be made. Nevertheless, we decided to
761   include it here, due to the overall similarities in the body shape and presence of the coloration
762   patterns of cuticle, like those in i.e. larvae of the group *Odontomyia* or other representatives of
763   Stratiomyidae (Supplementary figure 14). For these reasons we think that it is prudent to
764   consider this as a probable fossil of the Stratiomyidae, though there are no definite ways to
765   further support this. This morphotype is too poorly preserved for any detailed systematic
766   interpretation. Not much more information could be gained from the larvae, since the poorly
767   preserved body falls into the "unknown" habitat category of the morphospace.

768

769   *The fossil record of Stratiomyidae*

770   Given the important role of larval dipterans, their numerous ecosystem functions and their often

771   very specific association with certain microhabitats (Baranov et al., 2019), their fossil records

772   can provide a wealth of paleo-ecological information. Hence these new larval

773   stratiomyomorphan specimens widen our understanding of the respective paleo-ecosystems from

774   which they originated. Even on the adult side, representatives of Stratiomyidae are rare in the

775   fossil record, with only 73 occurrences (specimens) having ever been recorded (according to

776   PBDB, for the search parameters see Methods). This number is however excluding

777   representatives of a unique, extinct group of flies with the long proboscides (Zhangsolvidae),

778   known from the Early Cretaceous of China and Brazil, as well as Late Cretaceous of Myanmar

779   (Peñalver et al. 2015). These flies have emerged as important pollinators of the gymnosperm

780   plants in Cretaceous (Peñalver et al. 2015).

781   It is common for many organisms living in water to leave traces of their activity. Hence it

782   should not be surprising that in the deep past ichnofossils provide most of the geological record

783   of larval activity of Stratiomyidae, rather than body fossils. The most common example is the

784   Jurassic "ichnogenus" *Helminthopsis* Heer 1877. It was interpreted as originally caused by larvae

785   of soldier flies of the group *Stratiomys* Geoffroy, 1762 or at least a closely related species

786   (Mángano, Buatois, and Claps 1996). This expands the potential range of the geological record

787   of the group from the Barremian (Cretaceous) to the mid Jurassic (Mángano, Buatois, and Claps

788   1996; Pickerill, Han, and Jiang 1998). Body fossils of stratiomyomorphans, as mentioned, are

789   rare. All known larval fossil records are listed in Table 1, together with the material used in this

790   contribution. Myanmar amber seems to be particularly rich in stratiomyomorphan larvae, as the

791   number of morphotypes known from this deposit now has reached four. Liu et al. (Liu, Hakim,

792   and Huang 2020) have described two morphotypes of stratiomyomorphan larvae from this

793   amber. Both morphotypes are characterized by features intermediate between two

794   stratiomyomorphan ingroups, Stratiomyidae and Xylomyidae (Liu, Hakim, and Huang 2020).

795   Such chimera-like characteristics are also apparent in the one of the new morphotypes, namely

796   morphotype 1. It can be interpreted as a result of the "Push of the past" phenomenon (Budd and

797   Mann 2018). In contrast to morphotype 1, morphotype 2 from Myanmar amber has a much less

798   conspicuous morphology, and seemingly is a representative Stratiomyidae s. str. as characterized

799   by Hauser, Woodley, and Fachin (2017).

800   The record from Dominican amber, morphotype 3, is only the third record of the group

801   Stratiomyomorpha from this otherwise very productive deposit (Grund and Hauser 2005). Only

802   two specimens of the species *Pachygaster hymenea* Grund et Hauser, 2005 and a single

803   specimen of *Nothomyia* sp. (Poinar and Poinar 1999) has so far been reported from Dominican

804   amber. This could indicate that representatives of Stratiomyidae were either very rare in the

805   Miocene of Hispaniola, or alternatively their autecology was precluding them from being

806   preserved in amber (Solórzano Kraemer et al. 2018).

807   The   modern fauna of the isle of Hispaniola includes 13 species of Stratiomyidae

808   (Perez-Gelabert 2008). This relationship of fossil specimens to extant species is quite different

809   from the situation with another ingroup of Diptera: Chironomidae (non-biting midges). For
810   Chironomidae, there are more fossil species known from Dominican amber then there are extant
811   species on the entire island of Hispaniola (Grund 2006). The situation of Chironomidae in
812   Dominican amber can be explained by the fact that more attention was given to fossils of
813   Chironomidae of Hispaniola than to the extant ones. The same explanation cannot be applied to
814   the discrepancy in species richness of fossil and extant species of Stratiomyidae. Soldier flies are
815   mid- sized or even large flies; hence, they have a much lower chance of being overlooked in the
816   amber records than Chironomidae. Modern representatives of Stratiomyidae in the Neotropics
817   and other tropical regions are associated with open areas in the forests or forest canopy
818   (Woodley 2009; Hauser, Woodley, and Fachin 2017). We can therefore hypothesize that
819   Dominican amber was capturing primarily animals associated with tree trunks, rather than
820   canopy fauna or fauna of the open meadows within the forest. A similar capture pattern was
821   shown for the Madagascar copal (Solórzano Kraemer et al. 2018).
822   The cuticle fossil from Činžat (morphotype 4) originates from deep-water, low energy
823   sedimentary environment (Gašparič and Hyžný 2015). It is difficult to explain how a larva of
824   seemingly terrestrial Stratiomyidae ended up there. One possible explanation could be that the
825   specimen drowned with driftwood and other terrestrial debris (which are present in the deposit)
826   after a storm event.
827
828   The larva from Baltic amber is poorly preserved, and only identifiable as a larva of a
829   soldier fly by the presence of the coronet of setae on the rear end. Overall, the fossil resembles
830   extant aquatic larvae of the group *Odontomyia* (Supplementary figure 14 A, B), however, there
831   are not enough diagnostic characters for a conclusive identification (also see discussion above).
832   It is still conceivable that this specimen represents a species of Stratiomyidae with an aquatic
833   larva. There are several larval forms of Insecta that have an aquatic lifestyle and have been
834   recorded from Baltic amber. This includes immature of Odonata (damselflies), Ephemeroptera
835   (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies) (Wichard, Gröhn, and Seredszus
836   2009). Martínez-Delclòs, Briggs, and Peñalver (2004) suggested that aquatic larvae of Insecta
837   can well be entrapped by still sticky resin pouring into water. This was probably the case for the
838   larva from Baltic amber. This further supports that at least part of the Baltic amber deposits was
839   formed directly next to water, probably in a swampy environment (Wichard, Gröhn, and
840   Seredszus 2009).
841
842   The possible record of larvae of Stratiomyinae from the Eocene of the former maar Lake
843   Messel might represent a rare find of aquatic insect larvae from this deposit. Unfortunately, the
844   larvae are too poorly preserved for the detailed interpretation. Aquatic insects are generally rare
845   in the oil shale of Messel and in other maar lake deposits, because the fossil-bearing sediments
846   (the so-called oil shale) formed only in the deeper parts of the former maar lake, not in its shore-
847   region (Wedmann 2018). Aquatic insects, such as some larvae of Stratiomyidae were living in
848   the shallow water in the shore region, and they could be only preserved as fossils when they
849   drifted into the deeper, anoxic parts of the meromictic lake where the oil shale was formed.

850
851 *Eco-morphological consideration*
852

853 The ecomorphotype, or a shape of an organism adapted to a certain ecological condition, is used
854 here as a proxy for the diversity of forms within a group of organisms (Haug et al. 2020b).
855 Outlines of the entire body, or parts of it have been shown as superior proxies for the shape of an
856 organism in many cases, when landmarks are hard to define, or when such landmarks do not
857 reflect the shape of the organisms well enough (Tatsuta et al. 2018). One of the most often used
858 methods for the outline capture in geometric morphometry is a Fourier Elliptical Transformation
859 (Tatsuta, Takahashi, and Sakamaki 2018; Polášek et al. 2018). This method allows accessing the
860 diversity of ecomorphotypes of a group of organisms by examining body outlines. Here we used
861 all available fossil and extant Stratiomyomorpha larvae to trace the changes in the larval
862 morphospace occupancy of the group and, consequentially indirectly, ecological diversity
863 throughout its history.
864

865 *Ecomorphology of extant stratiomyomorphan larvae*
866 New material examined in this study has shed a light on the far greater larval diversity of the
867 group Stratiomyomorpha in deep time than was expected from the previously known geological
868 records. We analyze the diversity of the ecological morphotypes of stratiomyomorphan larvae
869 through time comparing it to modern ecomorphotype diversity. Here we use ecomorphotypes as
870 a stable shape of an organism that evolved in response to certain ecological conditions (Rotheray
871 2019).
872 Stratiomyomorphan larvae are occupying three main types of habitats: 1) aquatic, 2)
873 terrestrial, mostly upper soil, leaf litter, and lower vegetation, and 3) living in wood, hence a
874 saproxylic lifestyle. Many of the extant larvae of Stratiomyomorpha, in particular larvae of
875 Pachygastrinae, are terrestrial saprotrophic and live under the bark of the dead wood (McFadden
876 1967; Marshall 2012).
877 Larvae of Pantophthalmidae are saproxylic, inhabiting living wood (Marshall 2012).
878 Many other larvae of Stratiomyidae (i.e. not those of Pachygastrinae), are occupying aquatic
879 habitats. In the fossil record, we have some indisputably aquatic larvae, i.e. larvae *Odontomyia*
880 sp. from Randecker Maar (Kühbander and Schleich 1994) or larvae of *Stratiomyia* from the
881 Holocene of Germany (Karl and Bellstedt 1989). The original habitats of other fossil larvae are
882 less clear (Whalley and Jarzembowski 1985; Liu, Hakim, and Huang 2020).
883

884 We have attempted to compare ecomorphotypes of the extant aquatic, terrestrial and
885 saproxylic stratiomyomorphan larvae with the morphotypes of the fossil larvae. In doing so we
886 hoped to elucidate the changes in the stratiomyomorphan larval morphospace through deep time,
887 as a response to the changing environmental conditions. Our analysis has shown that
888 stratiomyomorphan larvae are showing essentially four main morphotypes: 1) elongated aquatic
889 larvae, roughly circular to oval in the cross-section, as larvae of *Stratiomyia*, *Oxycera*,
890 *Odontomyi*a, 2) terrestrial and saproxylic larvae with spindle-shaped or cylindrical bodies (Figs.

891   14 A, B). Analyses of the shape distribution in morphospace have shown that thickness of the
892   body and shape of the body at the ends are determining separation of the morphotypes. These
893   two characteristics of shape are of the predominant importance, as they are making major
894   contributions into the Principal components (P.C.) 1 and 2. These two P.C.s are explaining
895   36.1% and 21.2% of the shape variability respectively (Figs. 14 A, B and Supplementary figure
896   15). It is important to note however, that no significant separation between the morphotypes
897   exist, as ascertained by a MANOVA test. P.C.1 and P.C.2 components have p>0.05, when the
898   type of the habitat is used as an independent variable for morphotypes separation. This is also not
899   surprising as "aquatic" and "terrestrial" groups of the larvae are overlapping broadly in the
900   general shape, and the "saproxylic" larvae morphotype is deeply nested in the "terrestrial"
901   morphospace (Fig. 14 A, B).
902
903   *Ecomorphology of fossil stratiomyomorphan larvae.*
904   The fossil larvae are widely distributed in the stratiomyomorphan morphospace (Figs. 14 A, B).
905   Most Cenozoic larvae (from Slovenian shale, Messel, and Baltic amber) fall within the area
906   occupied by modern forms. Also, some of the Cretaceous forms fall within the area occupied by
907   modern forms.
908   Morphotypes 2, 3, 4 as well as the larvae from Liu et al. (2020) firmly fell into the part of
909   the morphospace occupied by modern terrestrial ecomorphotypes (Figs. 14 A). The larva from
910   Baltic amber plots into the "aquatic" type habitats, as did the specimens from morphotype 1, due
911   to their elongated body (Fig. 14 A). Despite that, we are hesitant to claim that morphotype 1
912   larvae are aquatic. Specimens of this morphotype are lacking the tell-tale characteristics of
913   (most) extant aquatic stratiomyomorphan larvae, the coronet of "hydrofuge" setae (Rozkošný
914   1991). Additionally, the extremely high abundance of morphotype 1 larvae (at least by the
915   standards of the dipteran larvae in an amber deposit) can be explained by a possible close
916   association with tree trunks. It is possible that these larvae lived under the bark of trees, as seen
917   in many extant larvae of Stratiomyidae (McFadden, 1967, Marshall, 2012). It is well known, that
918   organisms associated with tree trunks in the amber forests had higher chance of being preserved
919   in amber (Solorzano-Kraemer et al 2018). On top of that, a rich set of the syninclusions present
920   in the amber piece PED-0031 together with morphotype 1 larvae is pointing towards the
921   terrestrial environment (Supplementary figures 2, 3). Such syninclusions include: a mite, a
922   possible scale insect, parts of other representatives of Insecta, a fly of the group Bibionomorpha,
923   a beetle larva, a spider and a millipede. This strongly indicates a terrestrial environment for
924   morphotype 1 larvae.
925   Only one of the morphotypes described by Liu et al. (2019) falls outside of the
926   morphospace occupied by the extant Stratiomyomorphan larvae (Fig. 14 B, Supplementary
927   figure 15).
928   Our analysis has shown that the morphospace of stratiomyomorphan larvae has become
929   significantly larger over time. Only a small part of the occupied area of the morphospace was
930   lost, when we consider the general body shape. We think that increase in the morphospace size

931 of the Stratiomyomorpha can be explained by the gradual diversification of the group from the
932 Late Cretaceous onwards as it was shown by Wiegmann et al. (2011).
933
934 Conclusions
935 The fossil record of dipteran larvae and pupae is generally skewed towards abundant forms from
936 low-energy sedimentary basins, such as lake environments (Rasnitsyn and Quicke 2002).
937 Therefore, groups with primarily aquatic immatures and high abundance, such as Chaoboridae
938 and Chironomidae are over-represented in the fossil record (Rasnitsyn and Quicke 2002;
939 Zherikhin, Ponomarenko, and Rasnitsyn 2008). Aquatic larvae of other dipteran ingroups, while
940 rare, have occasionally provided unprecedented insights into the evolution and palaeoecology of
941 the group (Whalley and Jarzembowski 1985; Chen et al. 2014).
942   Terrestrial larvae of Diptera have been until recently considered extremely rare (Grimaldi
943 and Engel 2005). Recent works, however, have shown that certain groups of terrestrial dipteran
944 larvae can be quite abundant, at least in amber (Baranov, Schädel, and Haug 2019). Therefore, it
945 is not entirely surprising to find new immature representatives of Stratiomyidae in Cretaceous,
946 Neogenic and Paleogenic ambers as well as in other types of fossil deposits. Further in-depth
947 studies of amber and compression fossils collections will certainly lead to more new discoveries
948 pertaining to larval biology of Stratiomyomorpha and other groups of Diptera.
949
950

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961

962

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1228   **List of figures**

1229   Figure 1. Morphology of larva of the group Startiomyidae, exemplified by a larva of *Pachygaster*

1230   *atra*. A) Ventral view, marked; B) dorsal view, marked. Abbreviations: *a1-a7* – abdomen units

1231   one through seven, ap – anal setae, asl – anal slit, as anterior spiracle, D1-D3 – dorsal setae 1-3,

1232   DL –dorsolateral setae, ep – eye prominence, hc – head capsule, L – lateral setae (of abdomen

1233   unit), L1-L2 – lateral setae (of trunk end), mp – maxillary palp, mt – metathorax, pt – prothorax,

1234   sa – subapical setae, v1-v4 – ventral setae one – through four (of the trunk end), VL –

1235   ventrolateral setae (of the abdomen units 1-7).

1236

1237   Figure 2. Larva of morphotype 1, specimen PED-0031-2. A) Ventrolateral view; B)

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1239   anterior spiracle; *pt* – prothorax, *mt* – metathorax, *a2-a6* – posterior trunk units 2-6, *te* – trunk

1240   end, *ps* – posterior spiracle.

1241

1242   Figure 3. Larva head of morphotype 1, specimen PED-0031-2. A) Lateral view; B) Lateral view,

1243   marked; C) Lateral view, line drawing. Abbreviations: *hs* – head soft tissues, *hc* – head capsule,

1244   *lb* – labrum; *la* – labium; *mk* – mandibular-maxillar complex, *ta* – tentorial arm, *mr* –

1245   metacephalic rode, *ct* – cut off through the part of the head capsule, *pt* – prothorax, *cc* – calcium

1246   carbonate pallet.

1247

1248   Figure 4. Larval head of morphotype 1, specimen PED-0152-2. A) Dorsal view, habitus; B)

1249   Ventral view, head; C) Ventral view, head marked. Abbreviations: *mp* – maxillary palp, *bm* –

1250   base of mandibular-maxillar complex ("grinder"), *lb* – labrum.

1251

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1254   *hc* – head capsule, *as* – anterior spiracle; *ms* – mesothorax, *mt* – metathorax, *a1-a7* – posterior

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1256

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1260   head marked, LACM ENT 366281-2. Abbreviations: Abbreviations: *hs* – head soft tissues, *hc* –

1261   head capsule, *lb* – labrum; *mk* – mandibular-maxillar complex, *ey* – eyes; *as* – anterior spiracle.

1262

1263   Figure 7. Morphotype 3, habitus, ventral, larva PED-0462. A) Habitus, ventral view; B) Habitus,

1264   ventral view, marked. Abbreviations: hc – head capsule, pt – prothorax, ms – mesothorax, mt –

1265   metathorax, a1-a7 – abdominal units 1-7, *te* – trunk end.

1266

1267   Figure 8. A-B) Fossil larvae of the group Pachygastrinae, morphotype 3, PED-0462 and C-D)

1268   head of larva of the extant species *Pachygaster atra* . A & B) Ventral view of the head capsule

1269   unmarked and marked; C & D) Ventral view of the head capsule unmarked and marked;
1270   Abbreviations: *an* –antenne; *as* – anal setae; *pt* – prothorax, *ey* – eyes; *lb* – labrum; *mp* – maxillar
1271   palp; *mb* – base of mandibular-maxillar complex ("grinder"); *v1*-3 – ventral setae 1-3, *la* –
1272   labium.
1273
1274   Figure 9. Speculative reconstruction of the habitus and habitat of the fossil larvaof the group
1275   Pachygastrinae, morphotype 3. Onychophora *Tertiapatus* sp stalking at the background. Artwork
1276   by Christian Mccal, reproduced with permission.
1277
1278   Figure 10. Pachygastrinae, larva, morphotype 4, PED-0463. A) Habitus, ventral view; B)
1279   Habitus, ventral view, marked. Abbreviations: *hc* – head capsule; *ey* – eyes; *as* – anterior
1280   spiracle; *pt* – prothorax, *ms* – mesothorax, *mt* – metathorax, *a1-a7* – posterior trunk units 1-7, *te*
1281   – trunk end, *ps* – posterior spiracle, *fc* – folded cuticle.
1282
1283   Figure 11. Pachygastrinae, larva, morphotype 4, PED-0463, head ventrally. A) Head and
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1286   anterior spiracle, *lb* – labrum; *la* – labium; *mk* – mandibular-maxillar complex.
1287
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1290
1291   Figure 13. Stratiomyinae, larvae, morphotype 6 (SF-MeI 4666). A) compression fossil, habitus;
1292   B) compression fossil, marked; C) overview. Abbreviations: *hc* – head capsule; *phc* –
1293   pharyngeal grinding mill; *pt* –prothorax; *mt* – metathorax; *a1-a6* – abdominal units; *te* – trunk's
1294   end.
1295
1296   Figure 14. Ecomorphospace occupied by extant and fossil larvae of the group Stratiomyomorpha
1297   . Both plots presenting the same morphospace, split by different grouping variables. Total
1298   captured variation = 57.3%; 36.1% at PC1 and 21.2 % at PC2. A) Morphospace split by larval
1299   habitat: green – saproxylic, violet – terrestrial, blue – "unknown" (fossils), red – aquatic; B)
1300   Morphospace split by the geological age/deposit of the larvae: blue – extant, magenta –
1301   Myanmar amber, the rest of the deposits are represented by the single labelled dots.
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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), VL –ventrolateral setae (of the abdomen units 1-7).

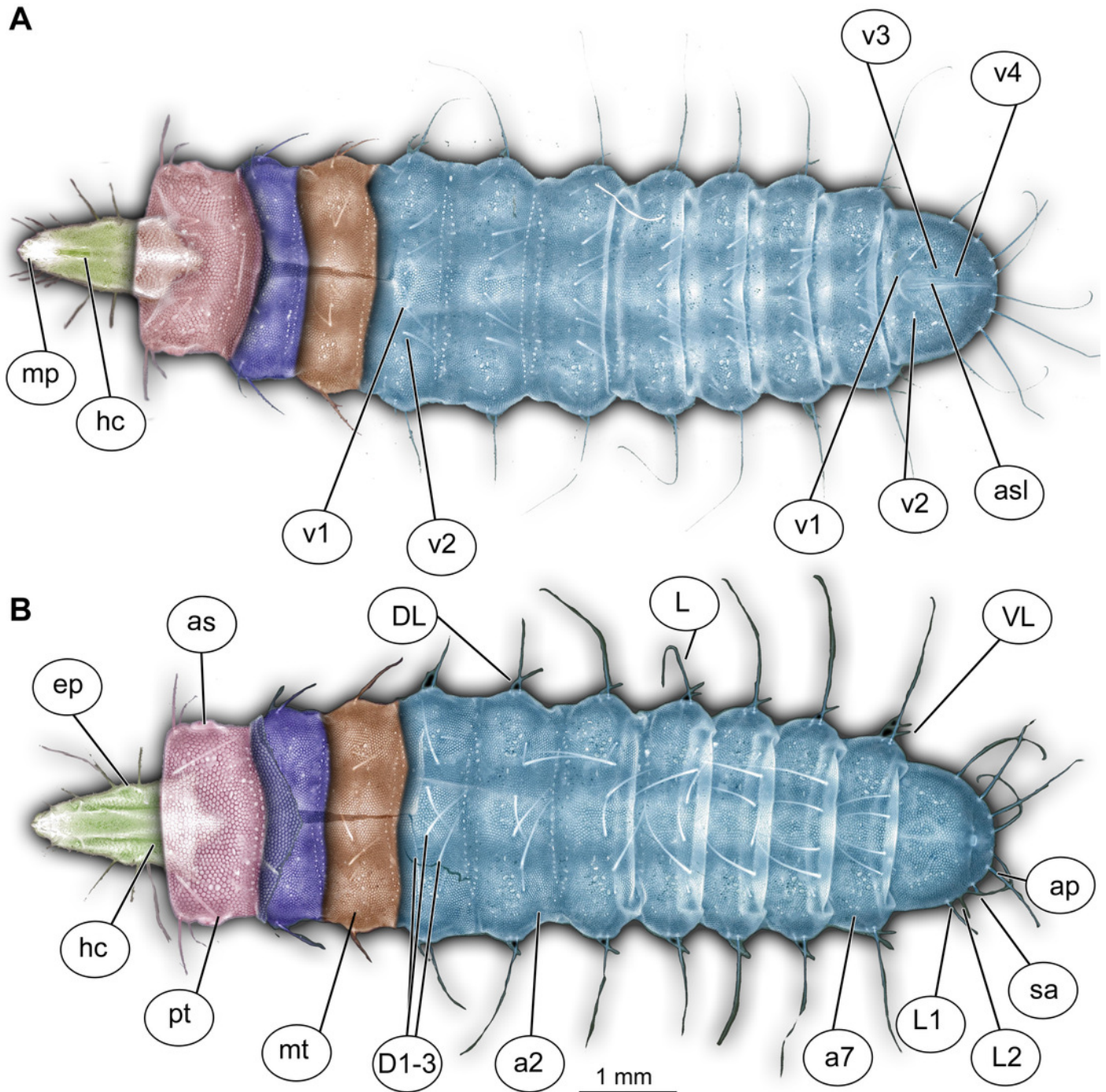



Figure 2

Larva of morphotype 1, specimen PED-0031-2

A) Ventro-lateral view; B) Ventro-lateral view, marked; C) Dorso-lateral view. Abbreviations: *hc*-head capsule, *as*-anterior spiracle; *pt*-prothorax, *mt*-metathorax, *a2-a6* - posterior trunk units 2-6, *te*- trunk's end, *ps* - posterior spiracle.

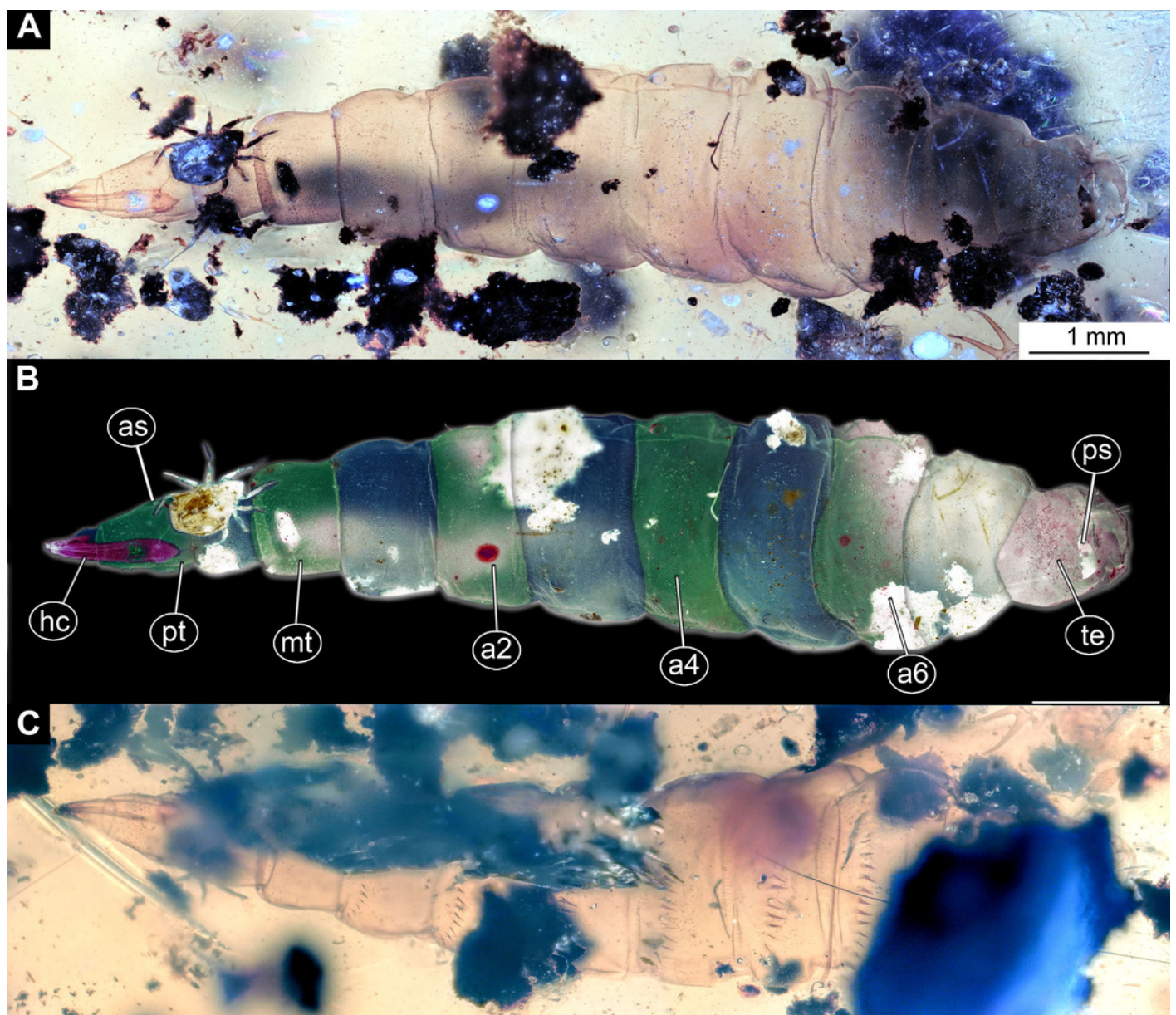



Figure 3

Larva head of morphotype 1, specimen PED-0031-2.

A) Lateral view; B) Lateral view, marked; C) Lateral view, linedrawing. 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.

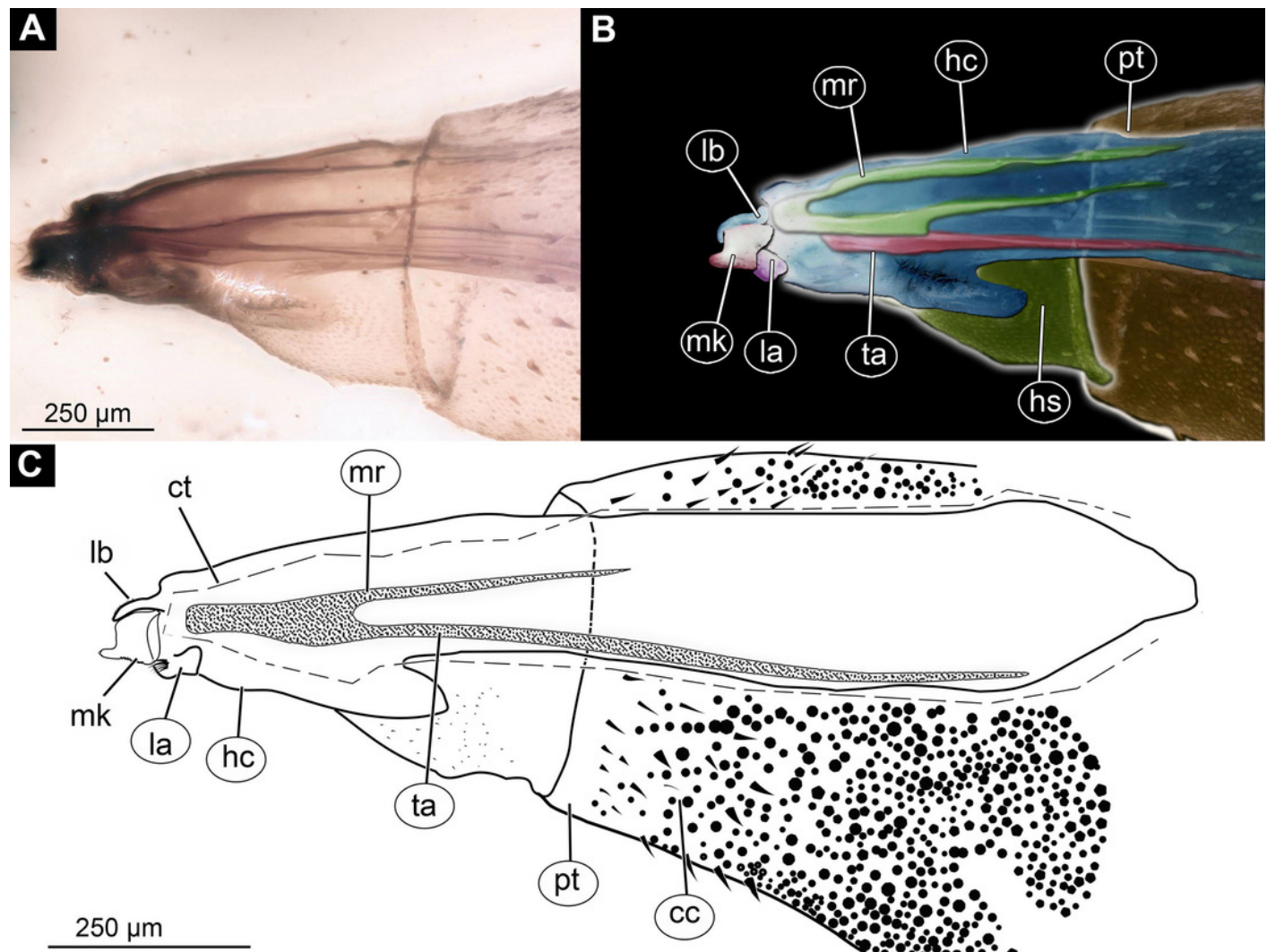



Figure 4

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.

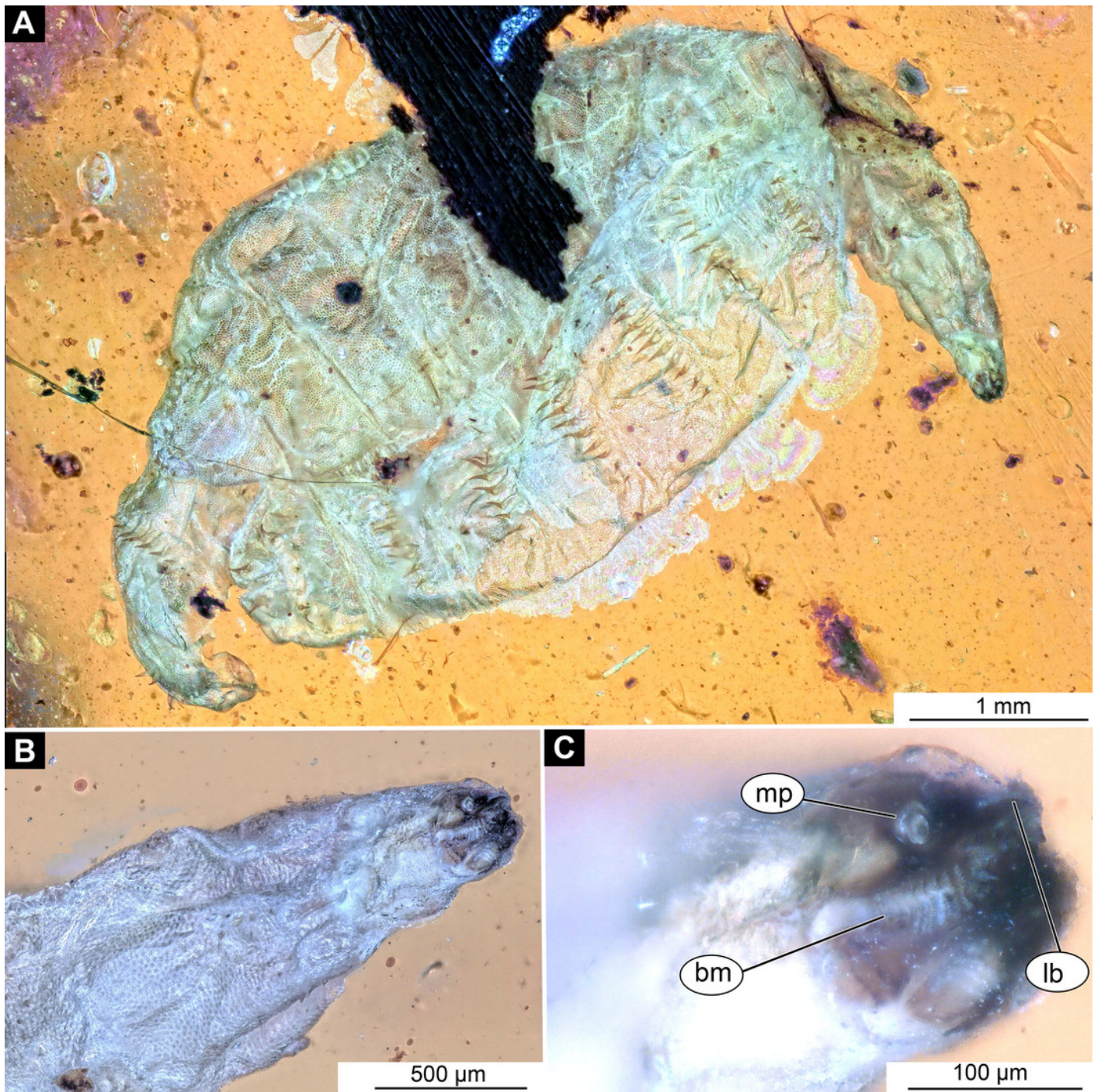



Figure 5

Larva of morphotype 2, specimen LACMALACM ENT 366281-1.

Figure 4. Larva of morphotype 2, specimen LACMALACM 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.

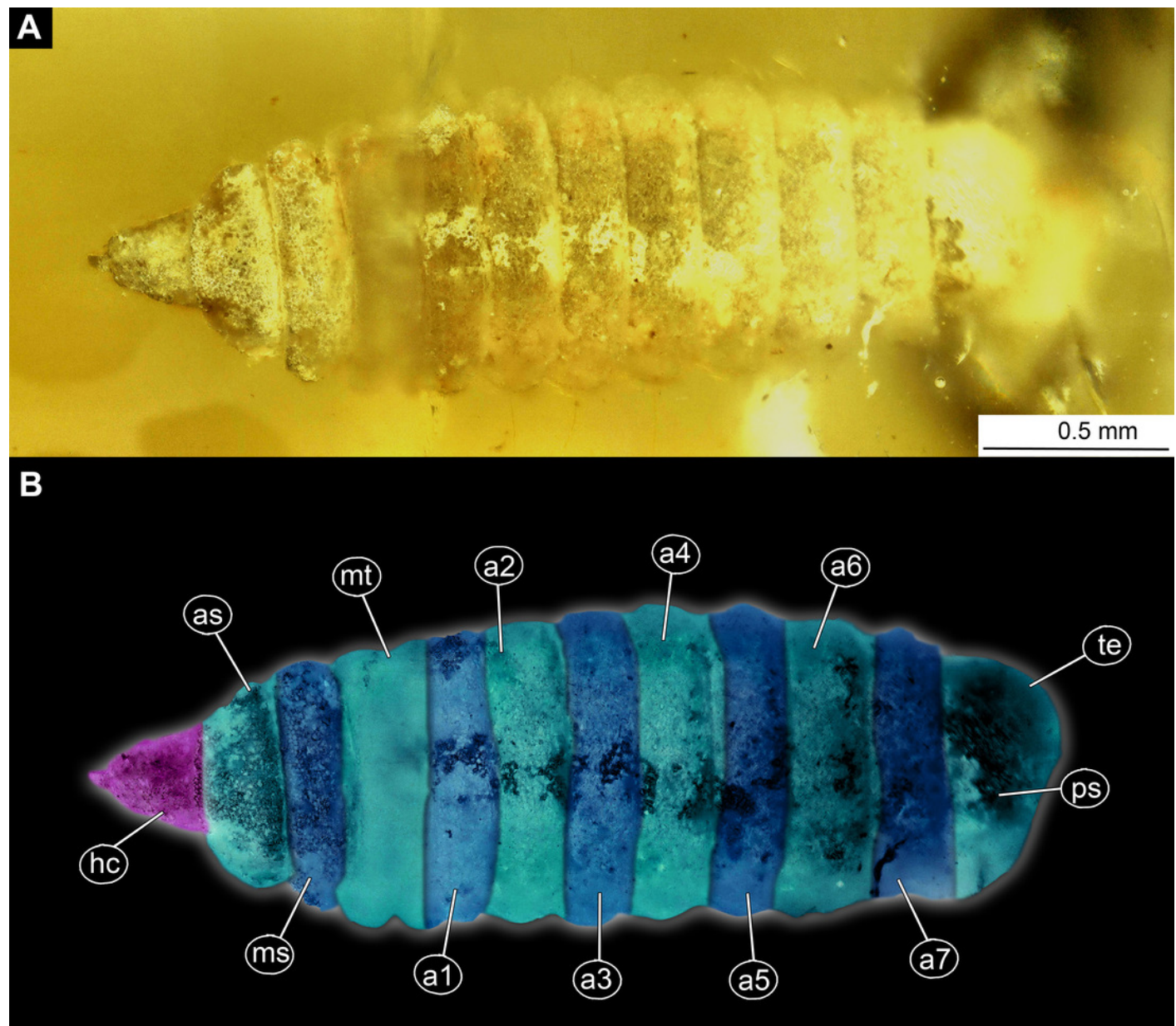



Figure 6

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: Abbreviations: *hs*-head soft tissues, *hc* - head capsule, *lb*-labrum; *mk* - mandibular-maxillar complex, *ey* - eyes; *as* - anterior spiracle.

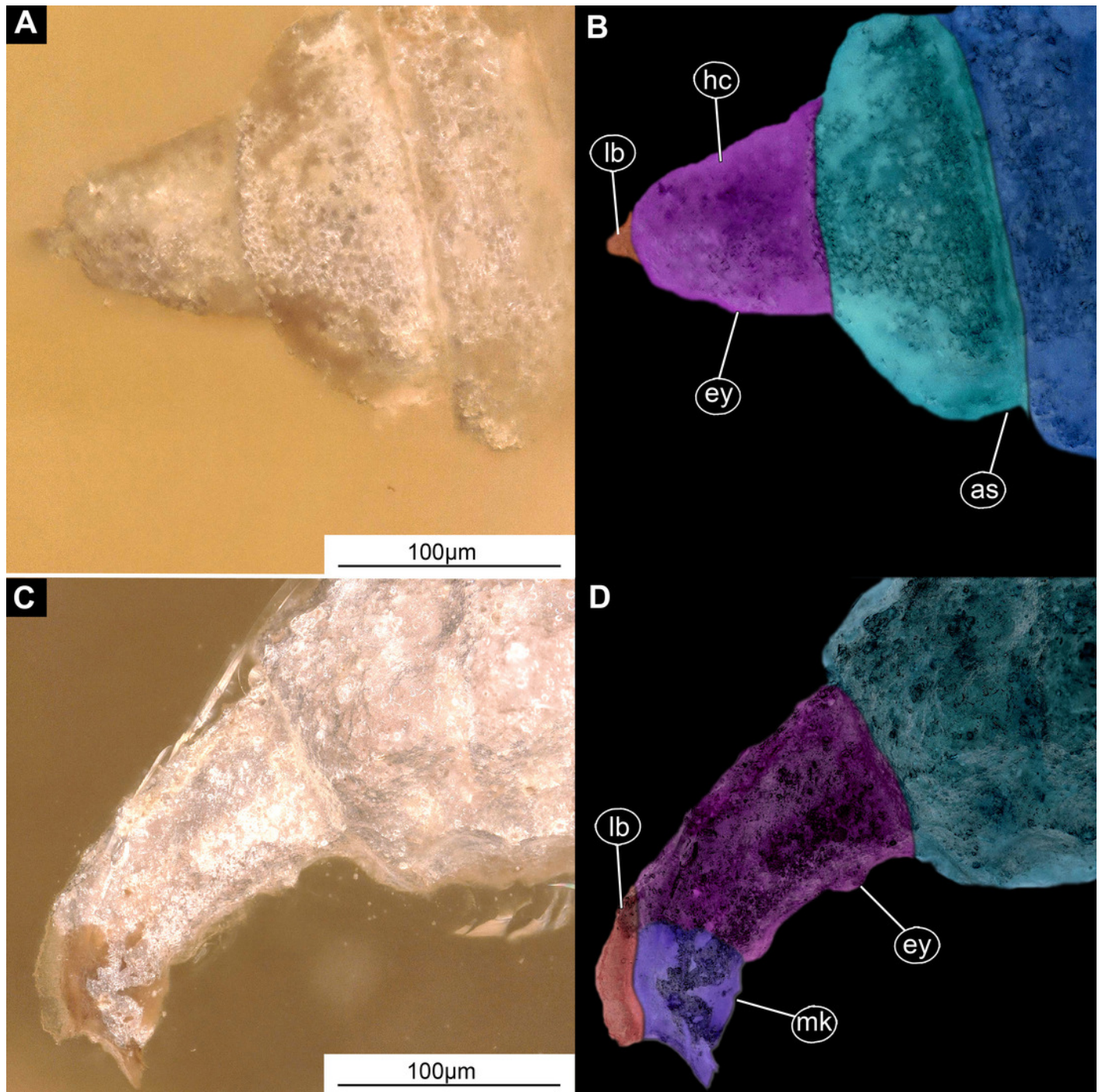



Figure 7

Morphotype 3, habitus, ventral, larva PED-0462.

A) Habitus, ventral view; B Habitus, ventral view, markes. Abbreviations: hc- head capsule, pt - prothorax, ms - mesothorax, mt -metathorax, a1-a7 - abdominal units 1-7, *te*- trunk's end.

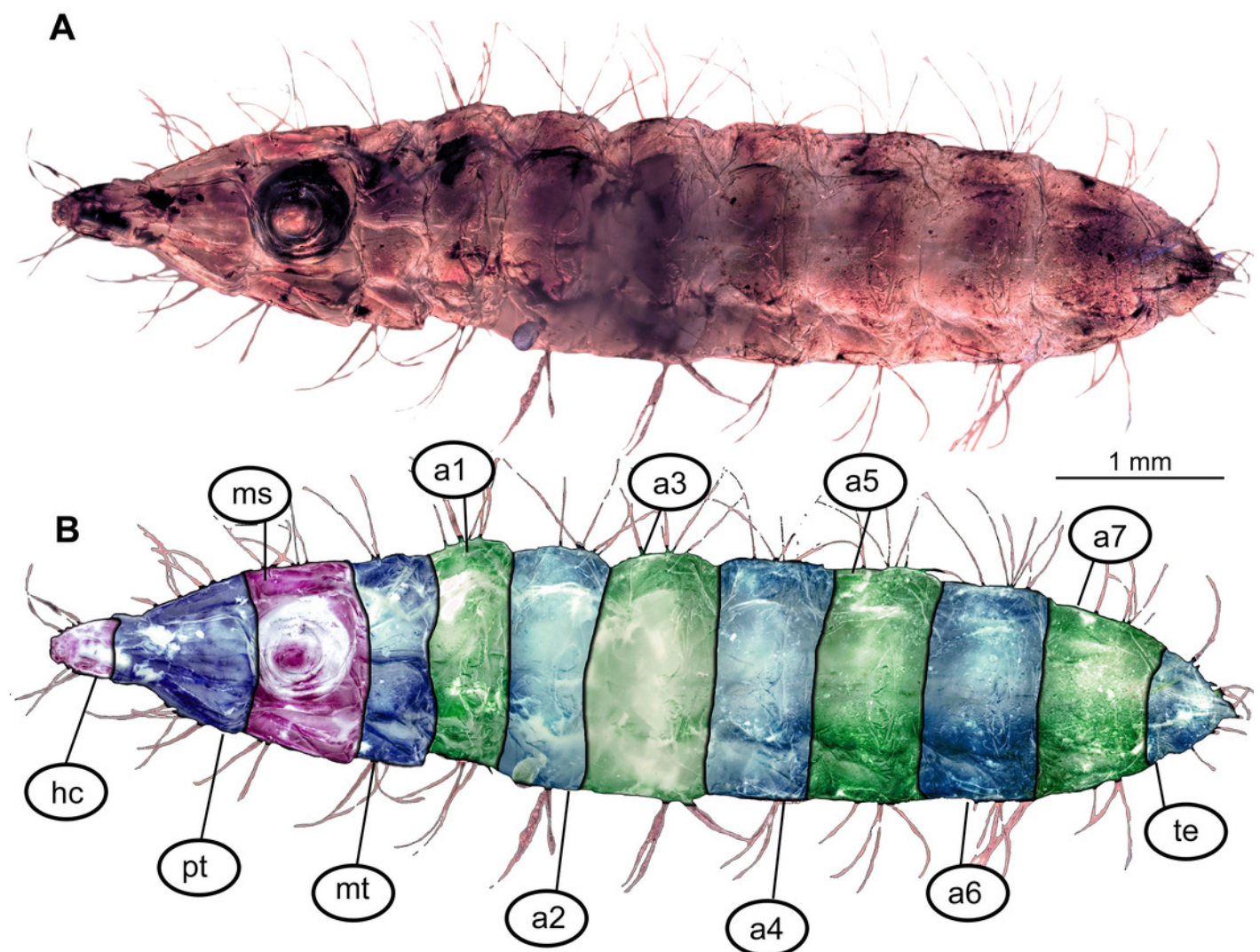



Figure 8

A-B) Fossil Pachygastrinae, larva of morphotype 3, PED-0462 and C-D), extant *Pachygaster atra, head.*

A & B) Ventral view of the headcapsule unmarked and marked; C & D) *Pachygaster atra*, Ventral view of the headcapsule unmarked and marked; Abbreviations: *an*-antenne; *as*- anal setae; *pt* -prothorax, *ey*-eyes; *lb*-labrum; *mp*-maxilar palp; *mb*- base of mandibular-maxillar complex ("grinder"); *v1*-3 - ventral setae 1-3, *la*- labium.

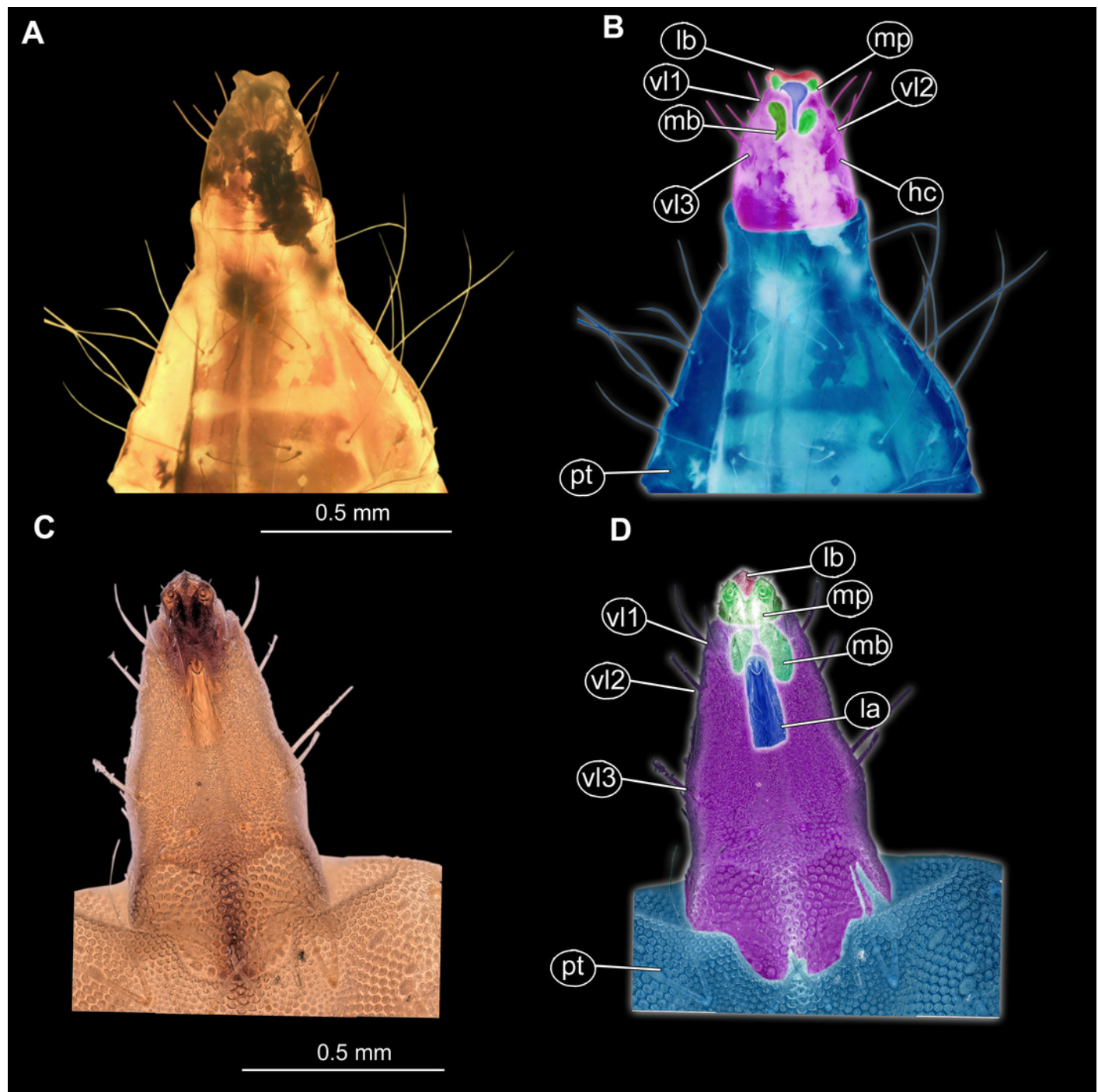



Figure 9

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 Mccall, reproduced with permission.

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's end, *ps* - posterior spiracle, *fc* - folded cuticle.

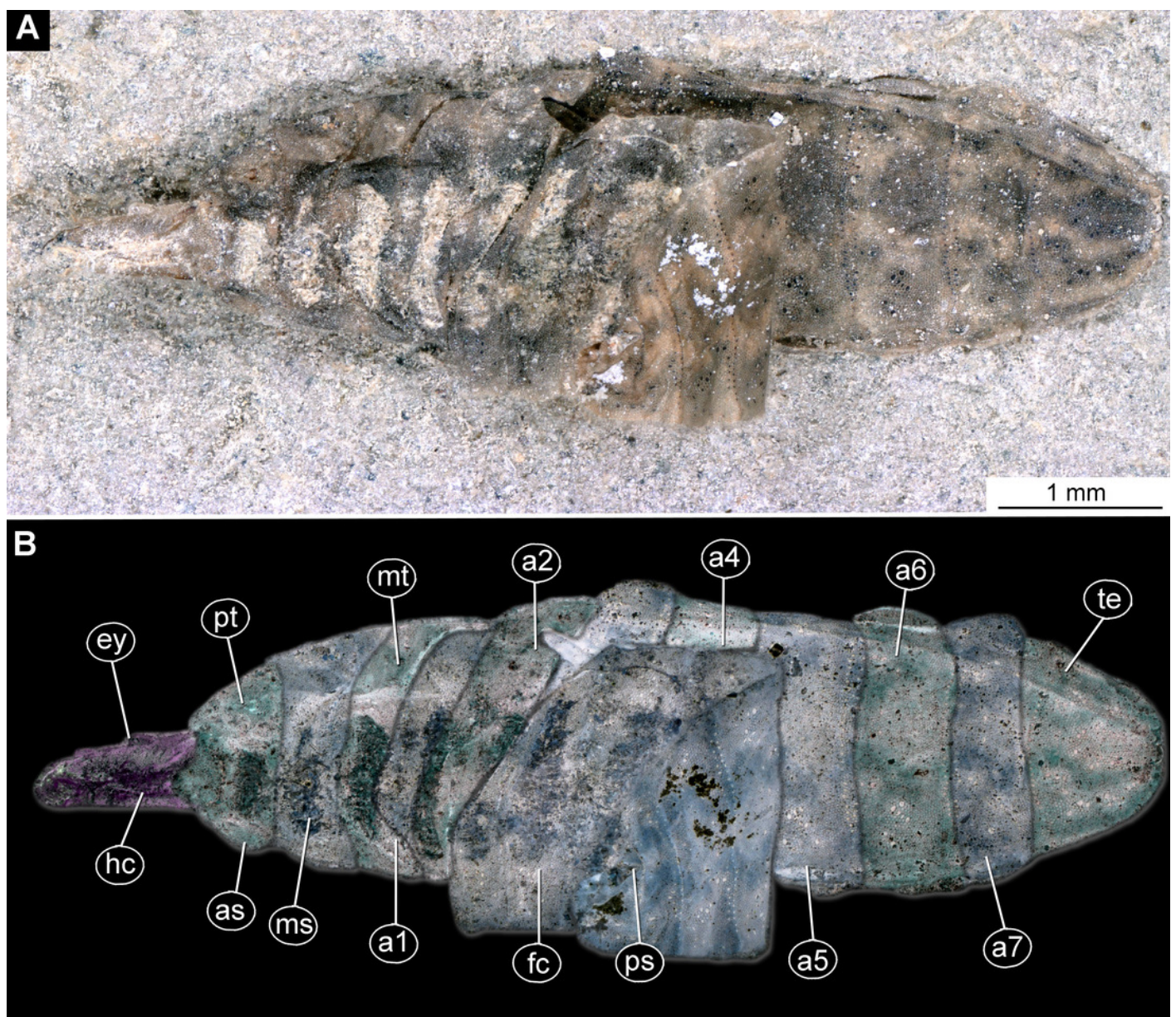



Figure 11

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.

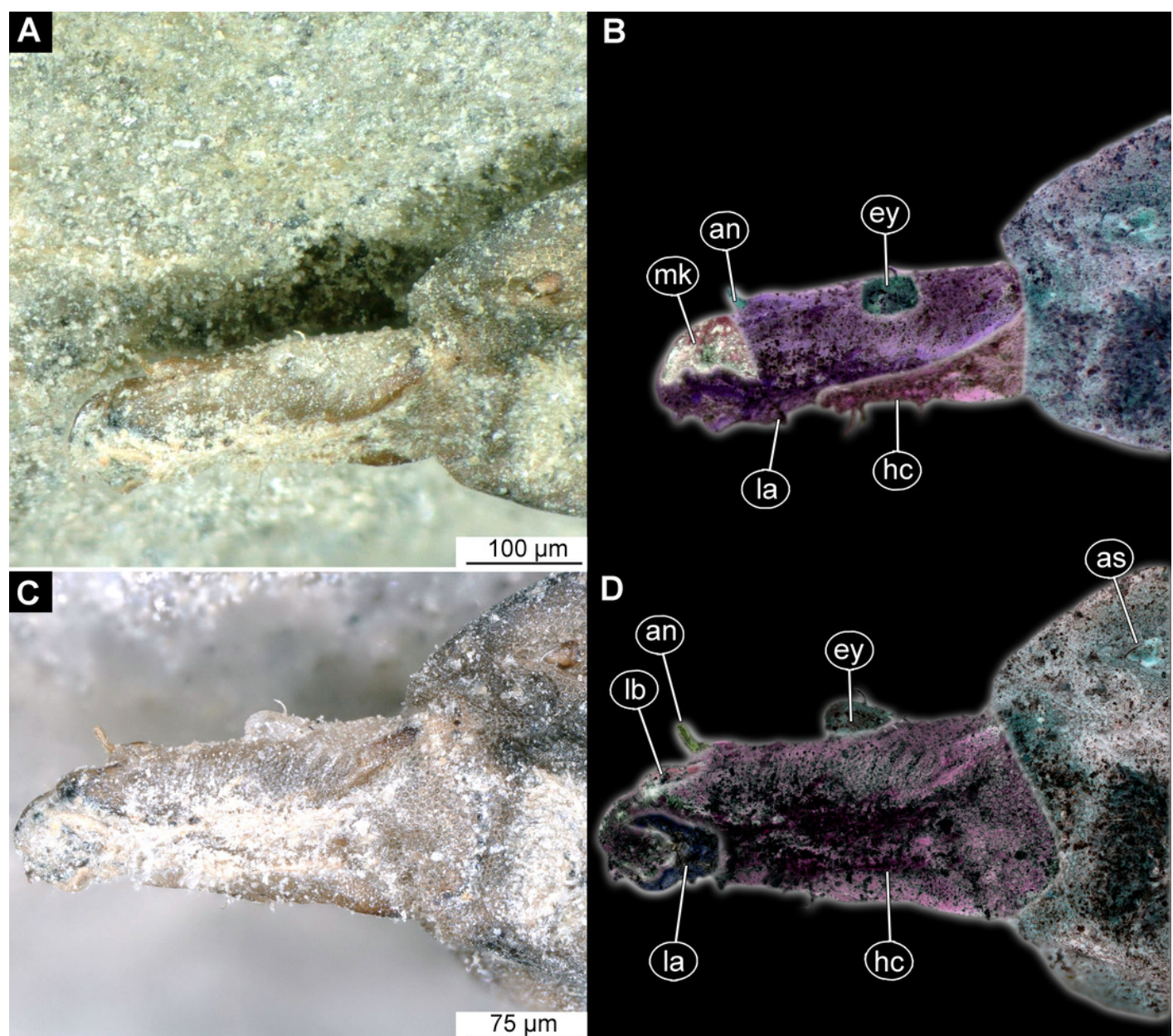



Figure 12

Fossil Stratiomyinae larva, morphotype 5 (PED-0464).

A) Habitus; B) Close-up photo of coronet of the hydrofuge setae.

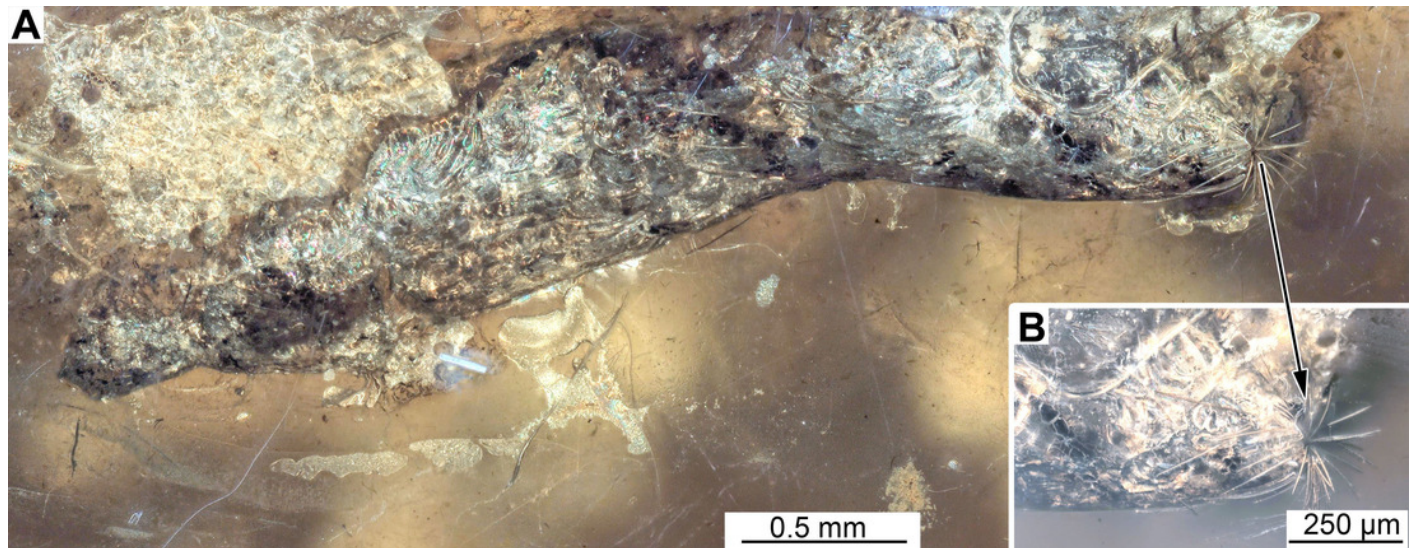



Figure 13

Fossil stratiomyinae larvae, morphotype 6 (SF-MeI 4666).

A) compression fossil, habitus; B) compression fossil, marked; C) Messel shale with Stratiomyiinae larvae, SF-MeI 4666, overview. Abbreviations: *hc* -head capsule; *phc* - pharyngeal grinding mill; *pt*-prothorax; mt -methathorax; *a1-a6*-abdominal units; *te*- trunk's end.

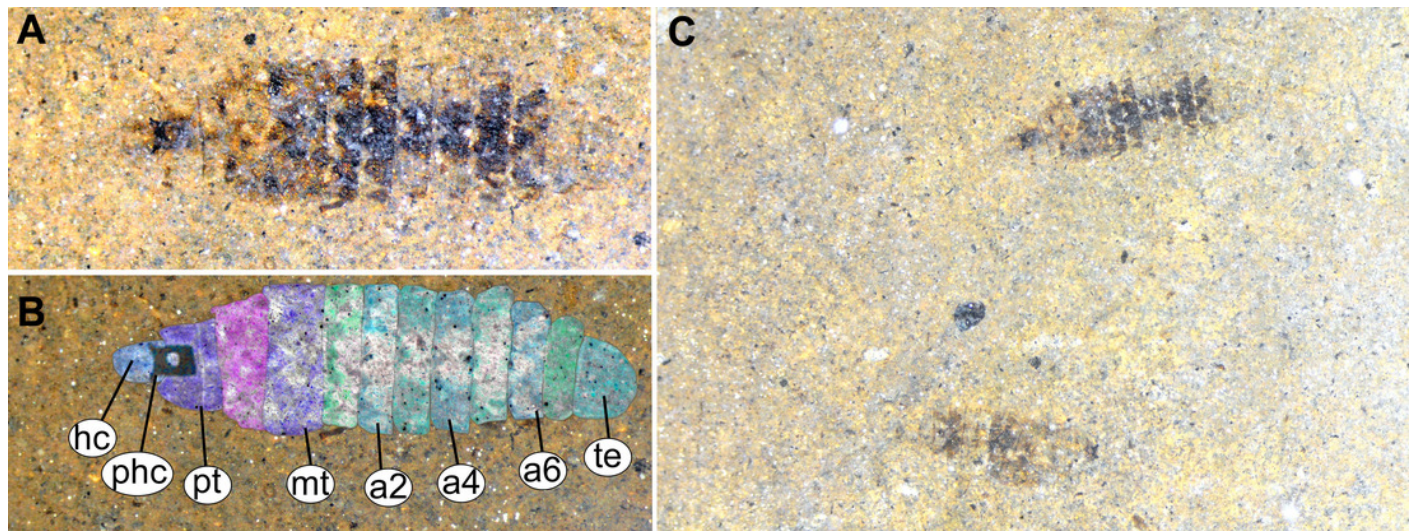
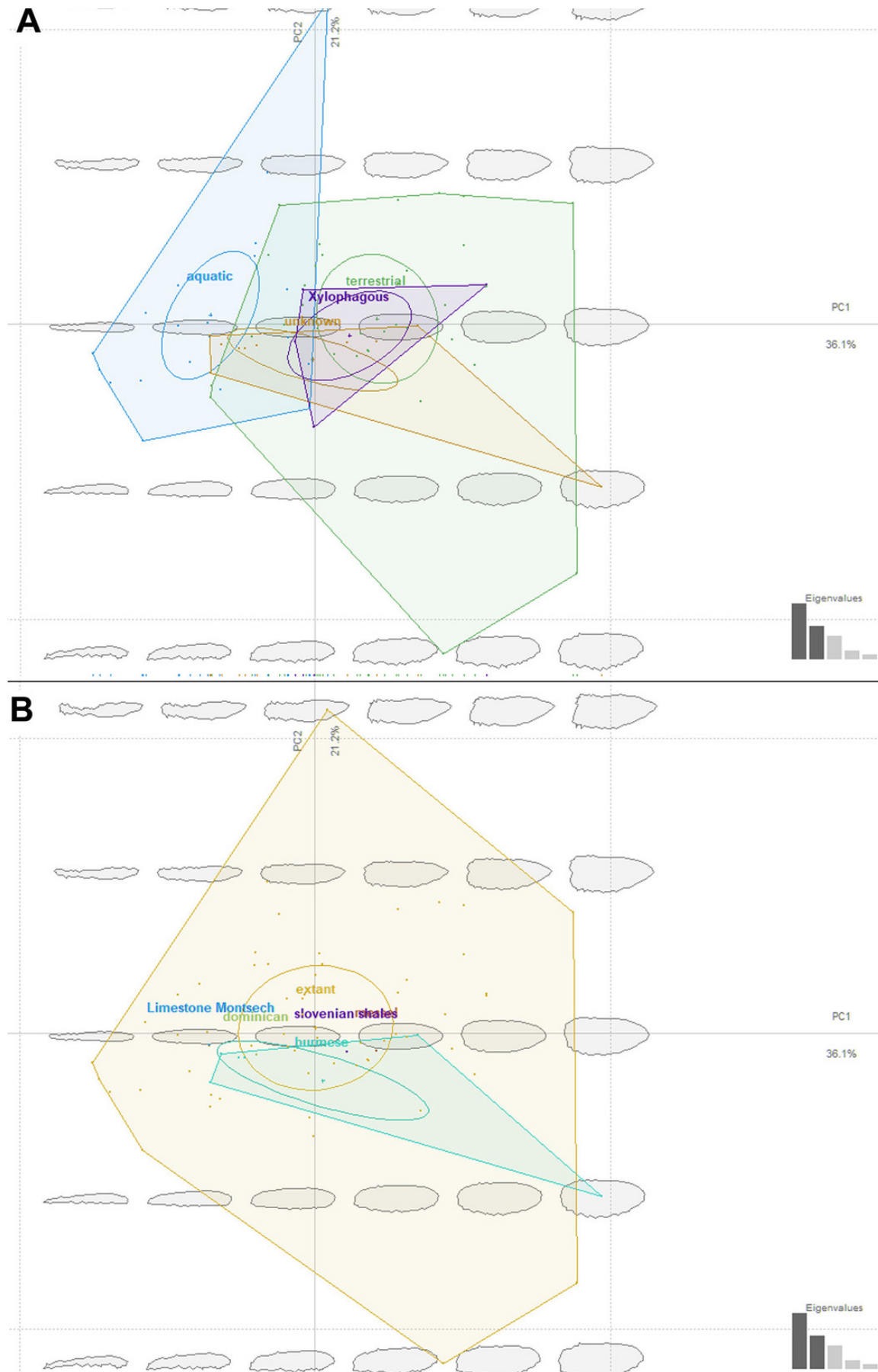



Figure 14

Ecomorphospace occupied by the extant and fossil Stratiomyomorpha larvae. Both plots presenting the same morphospace, split by the different grouping variables. Total captured variation = 75%; 62.1% at PC1 and 12.9 % at PC2.

A) Morphospace split by the larval habitat: violet - saproxylic, blue-terrestrial, green - "unknown" (fossils), red- aquatic; B) Morphospace split by the geological age/deposit of the larvae: blue - extant, red- burmese amber, the rest of the deposits are represented by the single labelled dots.

A

aquatic

terrestrial

Xylophagous

unknown

Eigenvalues

B

extant

Limestone Montsech   **slovenian shales**

dominican

burmese

Eigenvalues

Table 1. Material used in the paper.

Please note that ZSM does not provide numbers for most of their extant insect material, including specimens used in this article.

Taxon	ID number	Larvae	Syninclusions	Deposited at	Age
Morphotype 1	PED - 0152	3	NA	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 1	PED- 0349	1	NA	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 1	PED- 0362	1	Hymenoptera	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 1	PED- 0031	4	Diplopoda, beetle, 2 beetle larvae, collembola, aranea, probable scale insect, 2 mites	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 1	PED- 0041	1	NA	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 1	PED- 0243	1	NA	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 1	PED- 0113	1	NA	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 1	PED- 0025	1	NA	PED	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 2	LACM ENT 366281	5	NA	LACM	Cretaceous, Cenomanian 100.5 ± 0.4 MYA
Morphotype 3	PED- 0462	1	NA	PED	Miocene, 20.44- 13.92 MYA
Morphotype 4	PED- 0463	1	NA	PED	Miocene, 20.44- 15.97 MYA
Morphotype 5	PED- 0464	1	non-biting midge male (Diptera, Chironomidae); window-gnat (Diptera, Anisopodidae), two dark-winged fungus gnats (Diptera, Sciaridae), large spider (Araneae).	PED	Eocene, 37.8-33.9 MYA
Morphotype 6	SF-Mel 4666	2	NA	SF	Eocene, ca. 48.2 MYA

Pachygaster atra (Panzer, 1798)	not provid ed	>10 0	NA		ZSM	extant
Oxycera nigricornis Olivier, 1811	not provid ed	>10 0	NA		ZSM	extant
Odontomyia sp	PED-465	1	NA		PED	extant

2 Table 1. Material used in the paper. Please note that ZSM does not provide numbers for most of their

3 extant insect material, including specimens used in this article.