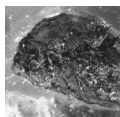


A group of assassin fly pupae preserved in a single piece of Eocene amber

JOACHIM T. HAUG, CHRISTINA NAGLER, CAROLIN HAUG & MARIE K. HÖRNIG



Holometabolous insects represent a mega-diverse group of organisms that are dominant in most terrestrial faunas. All holometabolous insects develop via a specific transitory stage between the last larval stage and the adult, called the pupa. While insects in general have a comparably good fossil record, fossils of pupae of holometabolous insects are relatively rare. We report here four pupal specimens preserved in a single piece of amber. These represent pupa stages of assassin flies, Asilidae, and are most likely representatives of Laphriinae. While dipterans are quite common in the fossil record, especially in amber, representatives of Asilidae are comparably rare. Combining the rarity of the systematic group and the rarity of the specific life stage, these fossil remains of assassin fly pupae are extremely unusual; to date only a single specimen has been depicted in the literature. We discuss the importance of our new finding and possible interpretations regarding behavioural aspects of the group enclosed in amber. • Key words: fossil pupa, Asilidae, Laphriinae, amber, fossilised behaviour.

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Joachim T. Haug & Carolin Haug, Ludwig-Maximilians-Universität München, Biocenter, Department Biology II, Großhaderner Straße 2, 82152 Planegg-Martinsried & GeoBio-Center of the LMU Munich, Richard-Wagner-Str 10, 80333 München, Germany; joachim.haug@palaeo-evo-devo.info, carolin.haug@palaeo-evo-devo.info • Christina Nagler, Ludwig-Maximilians-Universität München, Biocenter, Department Biology II, Großhaderner Straße 2, 82152 Planegg-Martinsried, Germany; christina.nagler@campus.lmu.de • Marie K. Hörnig, Ernst-Moritz-Arndt-Universität Greifswald, Zoologisches Institut, Cytologie und Evolutionsbiologie, Soldmannstraße 23, 17487 Greifswald, Germany; marie.hoernig@palaeo-evo-devo.info

Flying insects (Pterygota) represent a dominate life form on Earth. Within insects, the most diverse lineages are all ingroups of Holometabola, hence this group has been often named as the most successful ingroup of insects (however, this claim has also been applied to beetles, an ingroup of Holometabola). Holometabolous insects gained their name from a specific post-embryonic developmental pattern, which includes a so-called pupa.

The insect pupa

The pupa is usually understood as a kind of “intermediate”, mediating the transition from the larva to the adult (imago). The pupa is therefore often treated as something quite special. Yet, in other arthropod groups transitionary stages are known also, e.g. the megalopa in many lobster-like decapod crustaceans fulfils a comparable function (e.g. Rudolf *et al.* 2016 and references therein). In a wider view, the pupa can be seen as a highly specialised larval stage.

Immature stages of insects and also arthropods as a whole (including “classical” larvae, pupae, but also nymphs) tend to be considered less often scientifically than adults (e.g. Minelli *et al.* 2006). This applies to both extant and fossil forms. Fossil immature stages are more difficult to interpret in many cases, but have the potential to reveal important features that adult forms could not, and illuminate aspects of the life history, niche differentiation between adult and larva or the evolution of specialised larval forms (see more extended discussion in, e.g., Haug *et al.* 2013a, 2015a, 2016).

Fossil pupae

Insect pupae may also be quite rare in the fossil record, as well as being rarely described. Pupae that are aquatic have a higher potential to be preserved in sedimentary deposits than those from terrestrial forms, and several examples are known, for example, from limestones (e.g. Huguency *et al.*

1990, Johnston & Borken 1998, Davis *et al.* 2010, Lukashevich 2012, Lukashevich & Przhiboro 2015, see also references in Andersen *et al.* 2015).

Amber has great potential for preserving insects, but most commonly it is adults that are found. Larvae appear to be rare (though nymphs, in some groups, are quite widespread), and pupae seem even less abundant. Weitschat & Wichard (1998) in their large overview work only report pupae of lacewings (Planipennia), ants (Formicidae) and dipterans (Tipulinae; Anisopodidae). Pupae of ants in amber have also been reported by Brandão *et al.* (1998) and Perkovsky (2008). Ant pupae have a certain indirect mobility, due to the fact that they are carried around by their conspecific workers. Comparably, pupae of strepsipterans (Poinar 2004) have been found, and they are indirectly mobile due to their host.

The rarity even in amber (Andersen *et al.* 2015, Fischer 2015) is quite likely caused by the (largely) non-mobile pupae (but see above), and hence likely represents a true rarity, there might also be a certain “taxonomic bias”. The identification of pupae to a species is often challenging (*e.g.* Veltz *et al.* 2007), also in many extant groups pupae are often not described, making comparisons difficult. Nevertheless, fossil pupae have some potential to contribute scientifically (Lukashevich & Przhiboro 2015; see also above).

Lifestyle of Asilidae

Asilidae (assassin flies) is a group of dipteran, holometabolous insects with currently more than 7,000 described species (Pape *et al.* 2011, Wolff & Lamas 2016) with a worldwide distribution (Hull 1962). Despite niche differentiation (Lavigne *et al.* 1978) concerning habitat (Dennis *et al.* 2008), and a specific flight period in the year (Cannings 1997), all asilids have certain common features concerning their lifestyle. Adult and immature asilid males and females feed on other arthropods, mainly insects (Musso 1978).

The adults prey on spiders, beetles, butterflies, bees, wasps and other insects. They inject saliva containing neurotoxic and proteolytic enzymes into their prey (Wood 1981, Hayat 1997), which rapidly immobilises it and dissolves the tissue, allowing the assassin fly to feed on the liquid (Musso 1978). Larval forms are predatory or parasitic, mainly on beetle larvae (depending on the criteria for parasitism; more details in the discussion). The lifestyle of asilids has been interpreted to provide a healthy balance between insect populations in different habitats (Shurovnekov 1962, Joern & Rudd 1982).

Females lay their eggs in groups on leaves or stems of low-growing plants and grasses, in crevices, within soil (digging a hole with their ovipositor), under bark, or in burrows of wood-boring insects into dead wood (Cannings 1989). Some species, *e.g.* *Stichopogon trifasciatus*, *Machimus callidus*, *Efferia frewingi*, have been reported to

show a searching behaviour for a suitable place to deposit their eggs by investigating the possible oviposition sites with their ovipositors (Pritchard 1935; Lavigne & Dennis 1975, 1980; Dennis & Lavigne 1979; Dennis *et al.* 1986; Castelo & Corley 2004; Dennis 2012, 2013).

One factor for determination of the right oviposition site is the aggregation of possible hosts/prey larvae in the field (Castelo & Capurro 2000). The larvae are able to actively locate their hosts using chemical information provided by the hosts (Castelo & Lazzari 2004). The first instar larva of asilids, the so-called planidium (Musso 1981) can move and actively search for their hosts (Crespo & Castelo 2009). Similar location behaviour has also been reported for other dipteran larvae that are parasitic on different beetles (Godfray 1994, Brodeur & Boivin 2004).

Asilids have been found in the fossil record, but rarely (Dikow & Grimaldi 2014). Here we report a single piece of Eocene amber with four pupae identified as those of a species of Asilidae. We discuss possible affinities and biological interpretations of this find.

Material and Methods

Material. – The study is based on a single piece of amber, with four inclusions. The amber piece (FMNH PE 61074) is part of the collection of the Field Museum of Natural History in Chicago (FMNH). The amber piece is most likely of Baltic origin.

Methods. – Specimens (inclusions) were documented on a Leica DM 2500P compound microscope (Leica, Wetzlar, Germany) with a ScopeTek DCM 510 ocular camera. For reducing the optical deformation induced by the oblique surfaces of the amber piece, a drop of glycerol was placed onto the region of interest and covered with a cover slip, leading to a plane surface. One inclusion is broken and hence exposed on the surface; in this case no glycerol was applied.

For lighting, external cold light sources with light fibres were used for distributing light evenly from a low angle. Fibre lights were equipped with polarisation filters; these were cross-polarised with a polariser within the microscope to reduce reflections.

Due to the limited depth of field, stacks were recorded (several frames of the same image detail in different focal planes). Focal planes were shifted manually. Resulting stacks were fused using the software program Image Analyzer (MeeSoft, Michael Vinther). Fused images have more structures in focus than any of the single frames. Virtual surfaces based on the unsharpness of the images were calculated for certain specimens. Although this method may produce certain artefacts due to the transparency of the amber, it provides additional topological information of the specimen (for methods see also Haug *et al.* 2013b, 2015b; Hörnig *et al.* 2016).

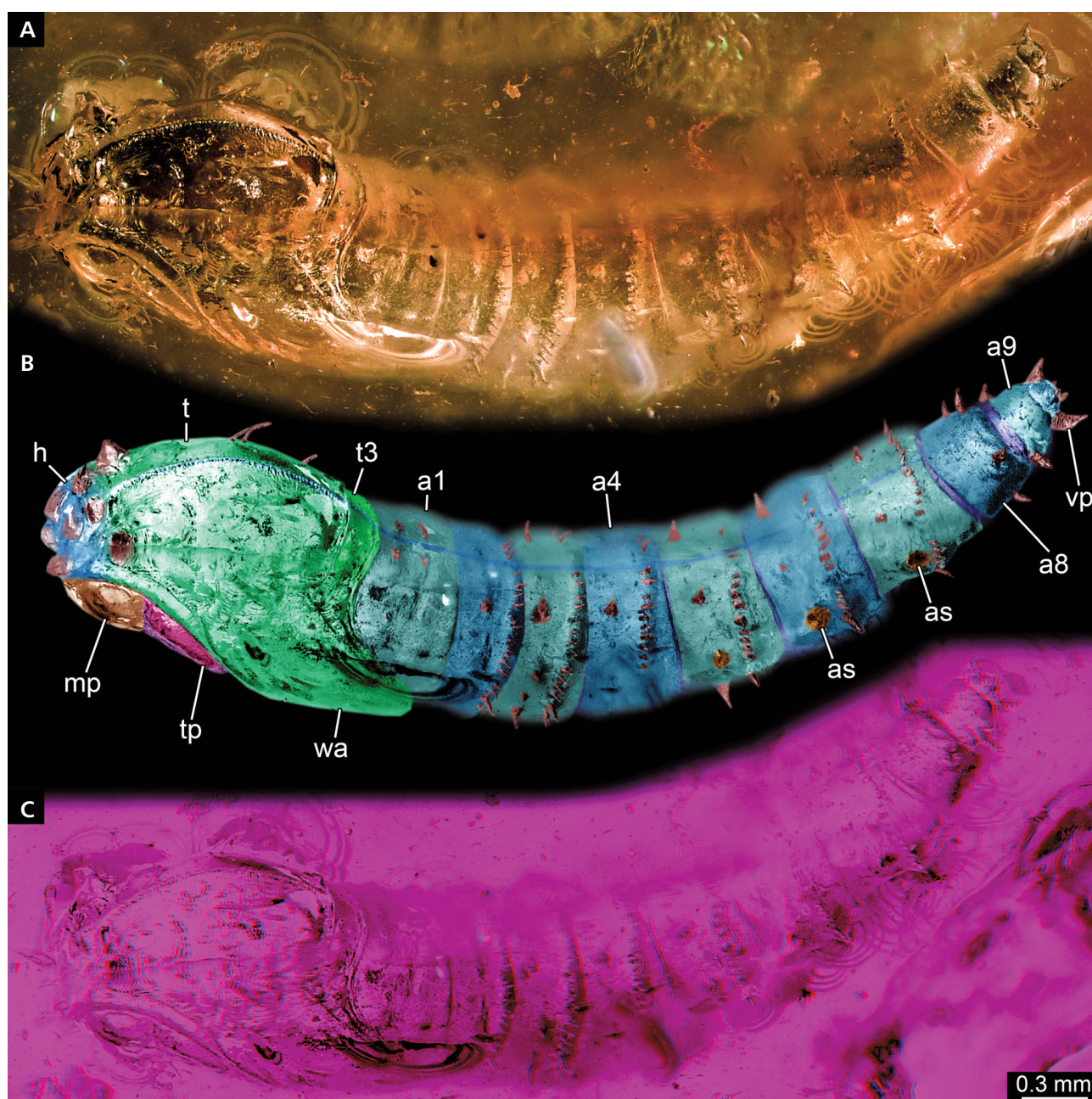


Figure 1. Specimen 1 of PE 61074. • A – overview image. • B – colour-marked version of A. • C – stereo image of specimen 1, please use red-cyan glasses to view. Abbreviations: a1–a9 = abdominal segments 1–9; as = spine of abdominal segment; h = head capsule; mp = mouthparts; t = tergites of first and second thoracic segment (without visible subdivision); t3 = tergite of third thoracic segment; tp = thoracopods; vp = ventral postero-lateral process; wa = wing anlage.

Results

Description of the amber piece

The amber piece has four major inclusions further described below as specimens 1–4. Furthermore, there are many additional small inclusions. These appear to be both plant remains and dirt particles.

Specimen 1

Preservation. – Amber surrounding specimen partly disturbed, most likely due to movements of specimen during embedding.

Orientation. – Largely lateral view on left body side, tilted slightly dorsally (Fig. 1).

Total body length 5.0 mm. Body organised into prominent anterior region (head and thorax) and posterior trunk (insect-type abdomen). Anterior region with weakly discriminated head region, anterior thorax region and distinct tergite of third thoracic segment (metanotum). Head region with vaguely visible blunt spine-like protrusions; further details not accessible due to disturbed amber surrounding this region.

Anterior thorax region without distinguishable subdivisions into tergites of first and second thoracic segment (pronotum, mesonotum). At anterior rim blunt spine (?) with three setae close to dorsal midline (on one body side, presumably same set on other side). Anterior two setae recognisable at about middle along anterior-posterior axis. Third seta at about three quarters along anterior-posterior axis. Dorsal outline of anterior thoracic region strongly convex. Dorsal midline of anterior thoracic region marked by slightly elevated crenulated crest. Antero-ventral outline of anterior thoracic region concave with slightly bulged rim. Postero-ventral outline of anterior thoracic region markedly drawn out postero-ventrally into lobate wing anlagen, partly covering succeeding segments. Tergite of third thoracic segment (metanotum) short, about 15% of length of anterior thoracic region. Lateral regions not observable, covered by wing anlagen.

Posterior trunk composed of nine or more segments. Abdominal segment 1 about 50% of length of anterior thorax region with two spines on each side close to midline at about midlength along anterior-posterior axis. Abdominal segment 2 shorter than preceding segment with length of about 30% of anterior thoracic region, with one prominent spine located dorso-laterally at about half way along anterior-posterior axis. At posterior edge prominent row of slightly backward curved spines; at least 18 spines on one side of body. Abdominal segment 3 slightly longer than preceding segment, length about 35% of anterior thoracic region, with one prominent spine dorso-laterally at about two-fifths of distance along anterior-posterior axis. More ventrally along this line three slightly smaller prominent spines. Posterior edge with prominent row of slightly backward curved spines; at least 14 spines on one side of body. Abdominal segment 4 slightly longer than preceding segment, more than 40% of length of anterior thoracic region, with one prominent spine dorso-laterally at about two fifths along anterior-posterior axis. Posterior edge with prominent row of slightly backward curved spines; at least 11 spines on one side of body. Abdominal segment 5 about as long as preceding segment, but slightly smaller in diameter, with one prominent spine dorso-laterally at about two-fifths of distance along anterior-posterior axis. Further ventrally along this line possible spiracle, even further ventrally one further prominent spine. Posterior edge with prominent row of slightly backward curved spines; at least 11 spines on one side of body. Abdominal segment 6 slightly longer than preceding segment, but slightly

smaller in diameter, with one prominent spine located dorso-laterally at about two-fifths of distance along anterior-posterior axis. Further ventrally along this line is a possible spiracle. Posterior edge with prominent row of slightly backward curved spines; at least 10 spines on one side of body. Abdominal segment 7 slightly longer than preceding segment, length about 45% of anterior thoracic region, but smaller in diameter, with one prominent spine dorso-laterally at about two-fifths of length along anterior-posterior axis. Further ventrally along this line is a possible spiracle. Posterior edge with prominent row of slightly backward curved spines; at least 11 spines on one side of body. Abdominal segment 8 shorter than preceding segment, length less than 30% of anterior thoracic region, but significantly smaller in diameter, with two prominent spines, one dorso-laterally, one further laterally, both relatively far posteriorly. Abdominal segment 9 shorter than preceding segment, length less than 25% of anterior thoracic region, significantly smaller in diameter, with two prominent spines (processes), one dorso-laterally, one further ventrally, both relatively far posteriorly. One additional spine on ventral side, larger in relation to preceding spines. Two additional smaller spines located far terminally.

Mouthparts postero-ventrally protruding from head. No details observable due to preservation. Thoracopods elongate and tube-like, on ventral side of thorax; no details available.

Specimen 2

Preservation. – Amber surrounding specimen partly disturbed, most likely due to movements of the specimen during embedding, but less than in specimen 1 (Fig. 2). Additionally, milky-appearing areas, possibly due to extrusion of gas.

Orientation. – Largely lateral view on left body side, tilted slightly ventrally.

Total body length 4.2 mm. Body organised into prominent anterior region (head and thorax) and posterior trunk (insect-type abdomen). Anterior region with only part of thorax region distinguishable (due to orientation of specimen). Head region not accessible due to orientation of specimen.

Anterior thoracic region without distinguishable subdivisions into tergites of first and second thoracic segment (pronotum, mesonotum). Dorsal outline of anterior thoracic region not accessible. Dorsal midline of anterior thorax region not accessible due to orientation of specimen. Antero-ventral outline of anterior thoracic region concave. Postero-ventral outline of anterior thoracic region markedly drawn out postero-ventrally into a lobate wing anlage, partly covering succeeding segments. Tergite of third thoracic segment (metanotum) not accessible due to orientation of specimen.

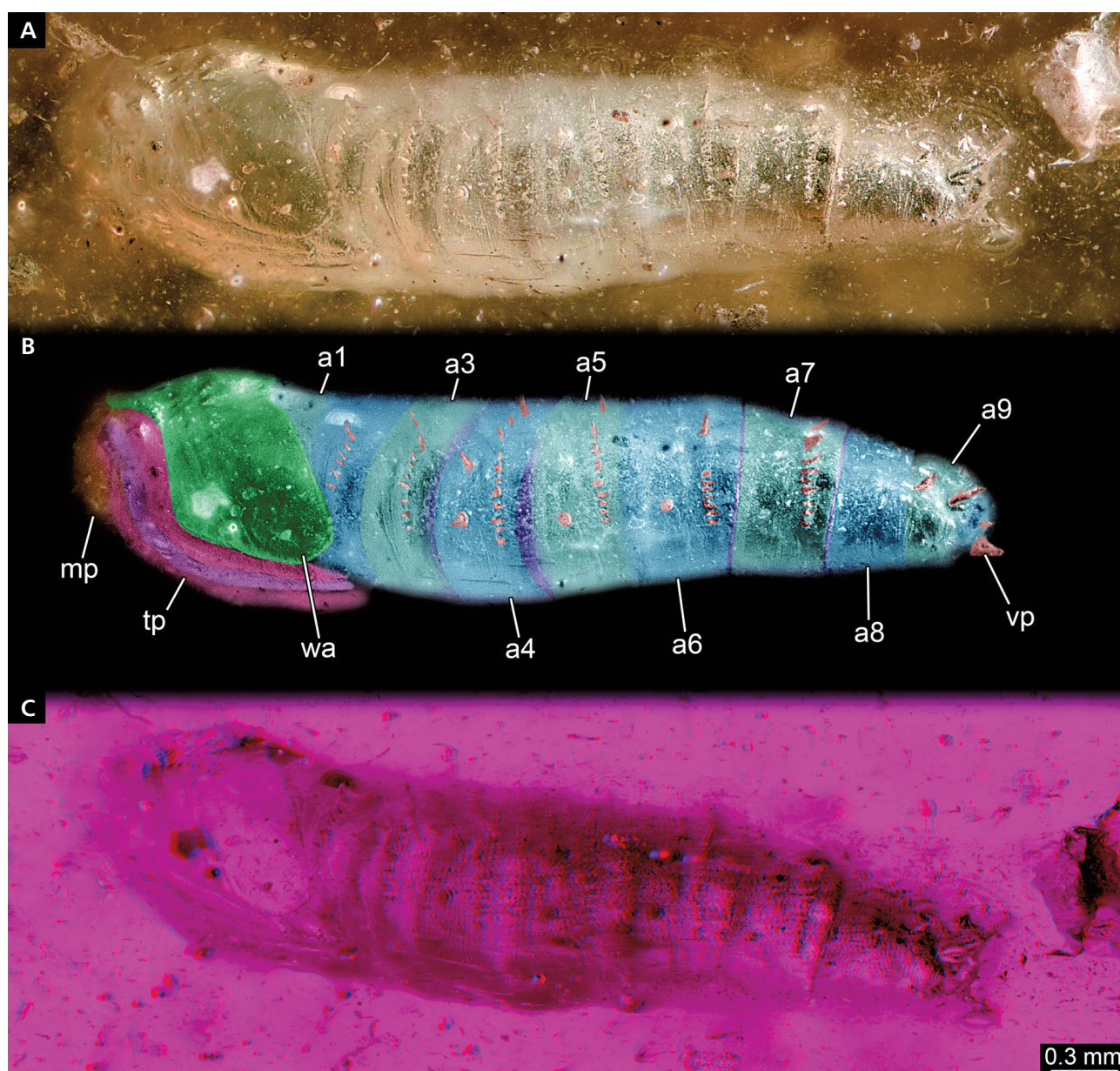


Figure 2. Specimen 2 of PE 61074. • A – overview image. • B – colour-marked version of A. • C – stereo image of specimen 2, please use red-cyan glasses to view. Abbreviations: a1–a9 = abdominal segments 1–9; h = head capsule; mp = mouthparts; tp = thoracopods; wa = wing anlage.

Posterior trunk composed of nine visible segments. Abdominal segment 1 about 50% of length of anterior thorax region. Abdominal segment 2 slightly shorter than preceding segment, exact length difficult to measure due to preservation. Posterior edge with prominent row of slightly backward curved spines; at least seven spines on one side of body. Abdominal segment 3 slightly longer than preceding segment, exact length difficult to measure due to preservation. Posterior edge with prominent row of slightly backward curved spines; at least 11 spines on one side of body. Abdominal segment 4 slightly longer than preceding segment, exact length difficult to measure due to preserva-

tion. With one prominent spine laterally at about middle along anterior-posterior axis. Further ventrally along this line one further prominent spine. Posterior edge with prominent row of slightly backward curved spines; at least 11 spines on one side of body. Abdominal segment 5 about as long as preceding segment, but slightly smaller in diameter, with one prominent spine ventro-laterally at about middle along anterior-posterior axis. Posterior edge with prominent row of slightly backward curved spines; at least ten spines on one side of body. Abdominal segment 6 slightly longer than preceding segment, but slightly smaller in diameter, with one prominent spine ventro-laterally at

about middle along anterior-posterior axis. Posterior edge with prominent row of slightly backward curved spines; at least 8 spines on one side of body. Abdominal segment 7 slightly longer than preceding segment, but smaller in diameter, with one prominent spine dorso-laterally at about two fifths along anterior-posterior axis. At posterior edge with prominent row of slightly backward curved spines; at least nine spines on one side of body. Abdominal segment 8 shorter than preceding segment and significantly smaller in diameter. Abdominal segment 9 shorter than preceding segment and significantly smaller in diameter, with a prominent spine (process) ventrally relatively far posteriorly. An additional smaller spine far terminally.

Mouthparts postero-ventrally protruding from head, poorly preserved. Thoracopods elongate and tube-like and situated on ventral side of thorax.

Specimen 3

Preservation. – Amber broken right through inclusion; inner side of inclusion largely exposed (Fig. 3). Amber surrounding specimen partly disturbed, most likely due to movements of specimen during embedding.

Orientation. – Largely lateral view on left body side.

Total (preserved) body length 4.4 mm. Body organised into prominent anterior region (head and thorax) and posterior trunk (insect-type abdomen). Anterior region with discriminated head region, anterior thorax region and distinct tergite of third thoracic segment (metanotum). Head region with vaguely visible protrusions; further details not accessible due to broken nature of this region. Anterior thoracic region without distinguishable subdivisions into tergites of first and second thoracic segment (pronotum, mesonotum). Dorsal outline of anterior thorax region strongly convex. Dorsal midline of anterior thorax region not accessible due to orientation of specimen. Antero-ventral outline of anterior thoracic region concave. Postero-ventral outline of anterior thoracic region markedly drawn out postero-ventrally into lobate wing anlage, partly covering succeeding segments.

Tergite of third thoracic segment (metanotum) short, about 15% of length of anterior thorax region. Lateral regions not observable, covered by wing anlagen.

Posterior trunk with at least six segments, posterior end not preserved. Abdominal segment 1 with about 50% of length of anterior thorax region, with two spines on one side close to midline at about middle along anterior-posterior axis. Abdominal segment 2 shorter than preceding segment, length about 30% of anterior thorax region, with one prominent spine dorso-laterally at about one third along anterior-posterior axis. Posterior edge with prominent row of slightly backward curved spines; at least three spines on one side of body. Abdominal segment 3 slightly longer

than preceding segment, length of about 35% of anterior thoracic region, with one prominent spine dorso-laterally at about one third along anterior-posterior axis. Posterior edge with prominent row of slightly backward curved spines; at least three spines on one side of body. Abdominal segment 4 slightly longer than preceding segment, length of more than 40% of anterior thoracic region and with one prominent spine dorso-laterally at about one third along anterior-posterior axis. Further ventrally along this line one further prominent spine. Abdominal segment 5 about as long as preceding segment, with one prominent spine dorso-laterally about one third along anterior-posterior axis. Further ventrally along this line one further prominent spine. Abdominal segment 6 incompletely preserved, no details accessible. Abdominal segments 7–9 not preserved.

Mouthparts postero-ventrally protruding from head; poorly preserved. Thoracopods elongate and tube-like on ventral side of thorax.

Specimen 4

Preservation. – Amber surrounding specimen heavily disturbed, most likely due to movements of specimen during embedding (Fig. 4). Additionally milky-appearing areas, possibly due to extrusion of gas.

Orientation. – Largely dorsal view, tilted slightly onto left side.

Total body length 5.0 mm. Body organised into prominent anterior region (head and thorax) and posterior trunk (insect-type abdomen). Anterior region with very weakly discriminated head region, anterior thorax region and vaguely distinguishable tergite of third thoracic segment (metanotum). Details of head region not accessible due to disturbed amber surrounding this region. Anterior thoracic region without distinguishable subdivisions into tergites of first and second thoracic segment (pronotum, mesonotum). Dorsal outline of anterior thoracic region not accessible. Dorsal midline of anterior thorax region marked by slightly elevated crenulated crest. Antero-ventral outline of anterior thorax region not accessible due to orientation of specimen. Postero-ventral outline of anterior thorax region difficult to access due to orientation of specimen. Tergite of third thoracic segment short, about 15% of length of anterior thorax region. Lateral regions not accessible due to disturbances in surrounding amber.

Posterior trunk composed of nine visible segments. Abdominal segment 1 about 50% of length of anterior thoracic region. Abdominal segment 2 slightly shorter than preceding segment; exact length difficult to measure due to preservation. Abdominal segment 3 slightly longer than preceding segment; exact length difficult to measure due to preservation. Abdominal segment 4 slightly longer than preceding segment; exact length difficult to measure due to

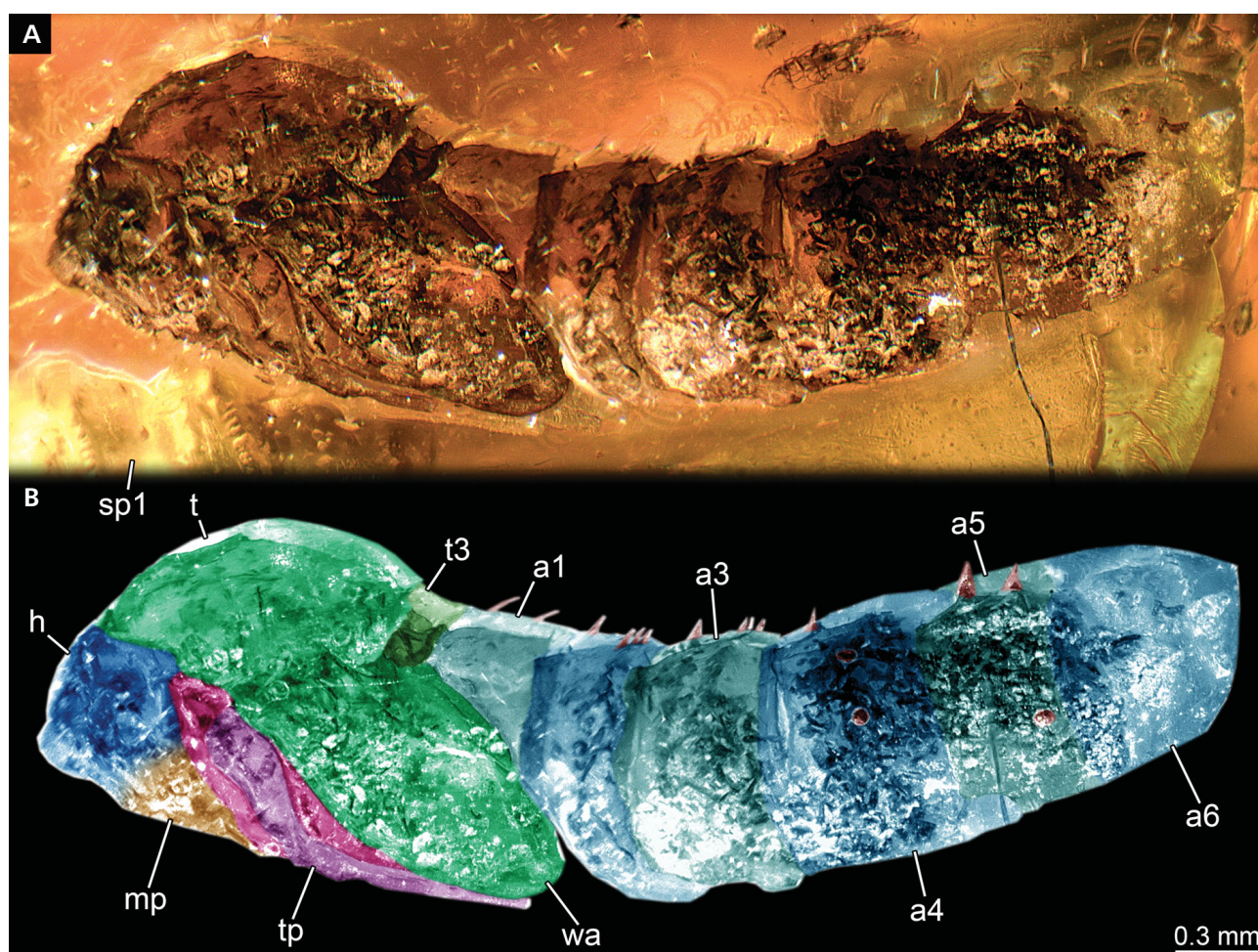


Figure 3. Specimen 3 of PE 61074. • A – overview-image. • B – colour-marked version of A. Abbreviations: a1–a6 = abdominal segments 1–6; h = head capsule; mp = mouthparts; t = tergites of first and second thoracic segment (without visible subdivision); sp1 = posterior part of specimen 1; t3 = tergite of third thoracic segment; tp = thoracopods; wa = wing anlage.

preservation. Posterior edge with prominent row of slightly backward curved spines; at least three spines on one side of body. Abdominal segment 5 about as long as preceding segment. Posterior edge with prominent row of slightly backward curved spines; at least five spines on one side of body. Abdominal segment 6 slightly longer than preceding segment; exact length difficult to measure due to preservation. Posterior edge with prominent row of slightly backward curved spines; at least four spines on one side of body. Abdominal segment 7 slightly longer than preceding segment, but smaller in diameter at posterior edge, with a prominent row of slightly backward curved spines; at least two spines on one side of body. Abdominal segment 8 shorter than preceding segment, significantly smaller in diameter, with prominent spine, one dorso-laterally accompanied by smaller spine. Abdominal segment 9 shorter than preceding segment, significantly smaller in diameter, with prominent spine (process) dorso-laterally relatively far posteriorly. Additionally, smaller spine far terminally.

Mouthparts not accessible due to orientation of specimen. Thoracopods not accessible due to orientation of specimen.

Discussion

Systematic interpretation

Based on the overall similarities among the four specimens we interpret them as conspecific; differences in observed features being most likely preservational. This accounts also for the body lengths as the specimens are preserved slightly bent and/or tilted in the amber, which complicates exact measurements. Also the perspective in which the specimens are accessible influences the visible length and may lead to underestimations.

Based on the overall morphology of the specimens they represent pupa stages (see schematic drawing in Fig. 5). As

the pupa is an autapomorphic character of Holometabola, the four specimens are immature holometabolans. The presence of a single pair of wing anlagen in all specimens indicates a position within Diptera.

A pupa with pronounced rows of spines on the abdominal segments is characteristic for Asilidae (Dennis *et al.* 2013). This is also compatible with the presence of stouter spines on the head (although not very well preserved in the fossil specimens). We tried to identify a more precise systematic position within Asilidae with the key of Dennis & Knutson (1988). These authors distinguished five major sub-groups (“subfamilies”): Leptogastrinae, Asilinae, Dasypogoninae, Megapodinae, and Laphriinae. Leptogastrinae is characterised by a pupa with hair-like structures instead of true spines on the abdominal segments and hence differs from the specimens described herein. Furthermore, Leptogastrinae is characterised by a pupa with a single pair of processes (spines) on the terminal abdominal segments, while in the described specimens there are at least two pairs.

The other asilid sub-groups have pupae with true spines on the abdominal segments and more than a single pair of processes on the terminal segment. Asilinae and Dasypogoninae are both characterised by a pupa with a longer dorsal process on the terminal segment. Laphriinae is characterised by a ventral process of the pupa, which is longer than the dorsal one seen in the described specimens. Megapodinae seems to be largely characterised by specifics of the head structures. As such structures are not easily observed in our specimens, we cannot find positive (nor negative) characters that would argue for (or against) a position of the described specimens in Megapodinae. While it is suboptimal that these characters cannot be taken into account, the morphology of the ventral process of the specimens gives a positive signal that the fossils are pupae of a representative of Laphriinae.

It is in general difficult to infer the relationship of a fossil based on keys for modern faunas, nor do keys offer a proper phylogenetic treatment. But it seems unlikely that a phylogenetic analysis of Asilidae incorporating pupal characters will be produced soon, which would be necessary to fully evaluate the fossils described here. We therefore see the use of modern keys as a reasonable (but sub-optimal) compromise.

Discussing the possible positions of the fossils within Laphriinae is challenging. One could argue that, as the fossils have been found in Europe, a key for European laphriine assassin flies should provide the best result. There are two shortcomings for such an approach: 1) The standard key for European species is provided by Melin (1923). Despite this work representing a kind of standard we were unable to access it. 2) Possibly more importantly, in the Eocene numerous insect groups were present in Germany that are now considered to be endemic in South

America, South Africa or Australia (see *e.g.* discussion in Wedmann *et al.* 2011 and references therein). Hence, the use of a key for species now present in Europe will not necessarily provide a better result than a key for other regions. For this reason and due to better availability we used the key provided by Dennis & Barnes (2013). The authors differentiate three major species groups (“genera”): *Lampria*, *Laphria* and *Andrenosoma*. According to the key, representatives of *Lampria* possess a pupa with a broad spine medio-dorsally on abdominal segment 1, which is bifurcate or trifurcate. This area is well preserved in specimen 1, but does not show such a spine. Hence, the specimens are probably not representatives of *Lampria*. Most other characters necessary for a further determination cannot be accessed in the fossil specimens. Hence, the specimens may be representatives of *Laphria* or *Andrenosoma*. We also cannot exclude the possibility that they are representatives of a now extinct lineage within Laphriinae, or even only closely related to Laphriinae.

Rarity of the find

As pointed out above, pupa stages of holometabolous insects are rare in the fossil record. Although dipteran fossils are very common (especially in amber), fossil findings of adult representatives of Asilidae are extremely uncommon (recently reviewed in Dikow & Grimaldi 2014). With this, our find of an assassin fly pupa is very exceptional.

The oldest possible (but partly controversial) fossil asilids known so far are from late Jurassic (Evenhuis 1994) and early Cretaceous (Grimaldi 1990). Among them are two species from the Crato Formation in Brazil (Grimaldi 1990, Grimaldi & Engel 2005) and two Burmese amber fossils (Dikow & Grimaldi 2014).

Further amber inclusions of asilid flies came from New Jersey amber (Grimaldi & Cumming 1999), Dominican amber and Malagasy copal (Scarborough & Poinar 1992, Dikow & Bayless 2009). Baltic amber has also yielded asilids (Schumann 1984, Geller-Grimm 1998, Gröhn 2015), including a single pupa (Gröhn 2015). The amber piece described herein is hence only the second report of a pupa of an asilid fly in the fossil record, possibly the first one of a species of Laphriinae, and is unique due to the fact that there are four specimens in one piece of amber. This latter aspect demands for further discussion.

Biological interpretation: Lifestyle of assassin fly larvae

The life style, specific developmental requirements and the morphology of assassin fly larvae is only known for two percent of the species of Asilidae, and even there only incom-

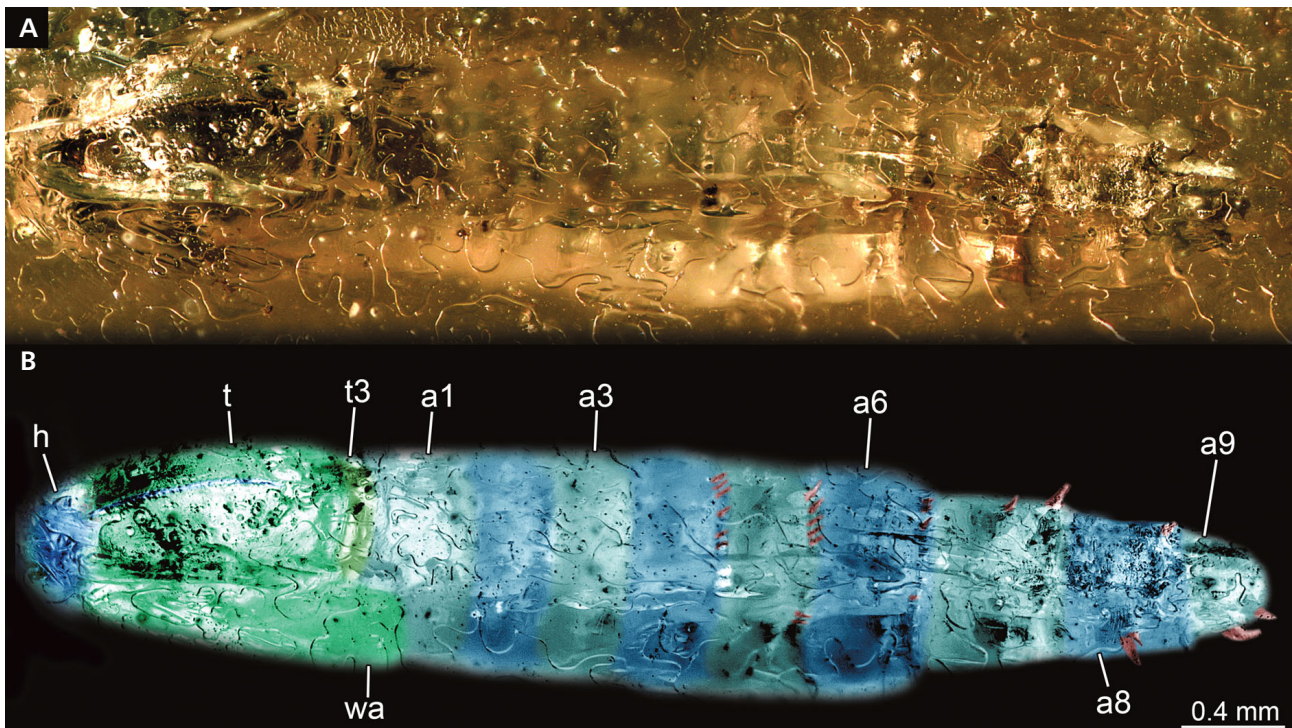


Figure 4. Specimen 4 of PE 61074. • A – overview-image. • B – colour-marked version of A. Abbreviations: a1–a9 = abdominal segments 1–9; h = head capsule; t = tergites of first and second thoracic segment (without visible subdivision); t3 = tergite of third thoracic segment; wa = wing anlage.

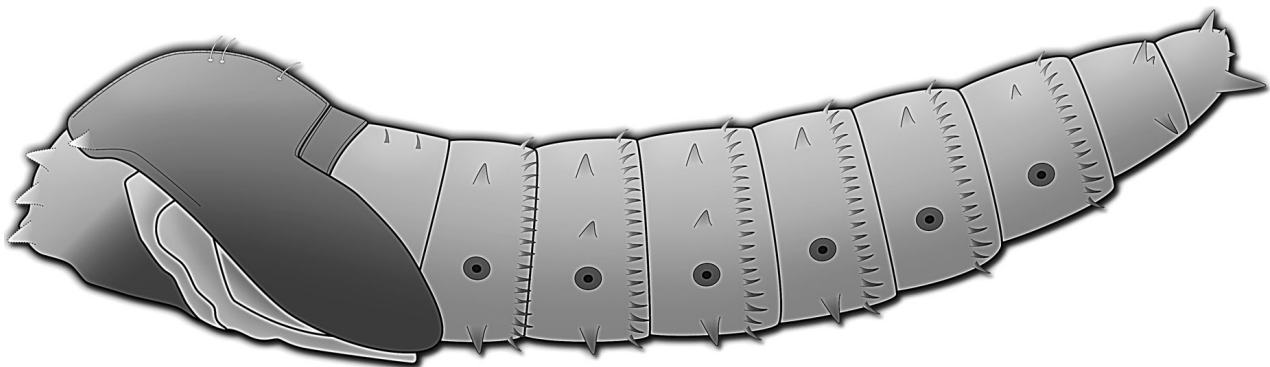


Figure 5. Schematic drawing based on pupal specimens of PE 61074.

pletely (Castelo *et al.* 2006, Dennis *et al.* 2008, Dikow 2009). What is known seems consistent throughout the group:

In general

Many assassin fly larvae are predatory or ectoparasitic (in the broad sense, see below) on immature stages of other insects in the soil or within dead wood (Knutson 1972, Dennis & Knutson 1988, Stubbs & Drake 2001). For example, the larvae of *Promachus yesonicus* are free-living predators of larval scarabaeid beetles. Larvae of *Mallophora ruficauda* also feed on larval scarabaeid beetles, but live attached to the host during their development (Castelo &

Capurro 2000, Castelo *et al.* 2006). The larvae have been reported to finally kill their hosts, when they are ready to pupate, thus assassin fly larvae are parasites in the broad sense, but more specifically should be considered as ectoparasitoids (Musso 1983). Important for understanding the fossils herein is the fact that if more than one parasitoid is attached to a single host (superparasitism), only one survives to reach the adult stage (Castelo *et al.* 2006, Castelo & Crespo 2012). After the larvae have pupated and completed development, the mobile pupa will move to the surface, and emerge after up to 20 days as adults, leaving behind their pupal case sticking vertically out of the soil (for soil-dwelling forms; Cannings 1997).

More specifically

Larvae of Laphriinae occur in rotten wood, especially in pines, but also in hollow fruit trees, aspen and spruce (Dufour 1850; Bromley 1934; Oldroyd 1972; Cannings 1989, 1997; Dennis & Barnes 2012). Not surprisingly, females of Laphriinae (but also Laphystiinae) are known for depositing eggs in groups into dead wood using their comparably long and cylindrical ovipositors (White 1916, Weiss & West 1922, Bromley 1934, Cannings 1997, Dikow 2009, Dennis & Barnes 2014).

Larvae of Laphriinae are also predators and ectoparasitoids, due to their habitat, especially on xylophagous insects (Lehr 1977, Geller-Grimm 2002). The larvae live in the galleries of wood-boring insects, such as those of weevils (Curculionidae) or wood wasps (Siricidae), and some produce their own galleries (Oldroyd 1972, Cannings 1997, Dennis & Barnes 2013). Overall, the larvae have been described as fairly active (Greene 1917). The non-free-living forms have been reported to be ectoparasitoids on the larvae of jewel beetles (Buprestidae) and longhorn beetles (Cerambycidae) that nest in tree stumps (Brauer 1883, Cerezke 1973, Fischer 1983, Dennis & Knutson 1988, Barriga 1990). Also in species of Laphriinae the pupae move to the surface (here of the dead wood) and the adults emerge (Bromley 1934, Musso 1967, Dennis & Barnes 2012, Dennis & Barnes 2014).

Biological interpretation: Do larvae of Laphriinae aggregate?

The amber piece with four pupae described herein has no indication of possible host/prey. A case of four assassin fly pupae occurring together is rather surprising, given the rareness of pupae and asilids in general, but also based on the life style of assassin fly pupae. Hence, the condition that leads to this co-occurrence is not immediately apparent. Based on observations of extant assassin fly larvae, it seems unlikely that the group was the result of active aggregation or gregarious behaviour of larvae unless the site offered ideal conditions for pupation.

Castelo & Capurro (2000) reported that female asilids choose their oviposition site based on the aggregation of possible host species. These authors concentrated on Asilinae and not on Laphriinae, but the information may still be relevant.

In the case of Laphriinae, the hosts are mainly larvae of xylophagous insects. One such group, longhorn beetles, have females that lay on average 120 eggs in a single tree stump (Donley 1978). On average, 600 longhorn beetle larvae have been reported alive per tree (Fierke *et al.* 2005). Longhorn beetles show a very carefully timed life cycle (Fierke *et al.* 2005). Coupled to this, this can be also assumed for asilids, further corroborated by a very limited

and specific flight period of many species within Laphriinae (Cannings 1997) and the triggered emergence of the pupae by temperature and light (Baker & Fischer 1975). Ritcher (1940) reported up to 40 predatory assassin fly larvae engaging a single beetle pupa. This means comparably high densities of assassin fly larvae and pupae in certain localities but within short time frames.

Based on the observation on extant relatives, we assume that the fossil pupae also developed from larvae feeding on larvae of xylophagous insects in dead wood, either as predators or as ectoparasitoids. We further speculate that several pupae emerged to the surface of the wood more or less at the same moment and rather close together. Presumably, the here described group was enclosed in this short time frame, by a drop of resin from a living tree.

Hence, this case of co-occurrence likely does not reflect active aggregation behaviour of the enclosed animals but more likely is the result of an association of individuals in a particular timeframe. The find represents an extremely unusual case and displays a poorly documented episode in the development of extinct assassin flies.

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