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Driven apart: fossil parasitic long-legged velvet mite larvae on gall midges represent a long lost parasitic association between mites and dipterans

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Abstract

Parasites are virtually ubiquitous, and this has probably been the case for quite some time. The record of parasitic mites (*sensu lato*) goes back as far as the Carboniferous (~359–259 mya) and, in fact, they are one of the most reported parasites in amber. The six-legged larvae of the mite group Parasitengona have a wide host range, among which are flies. Here we report for the first time cases of larval erythraeoidean mites, commonly referred to as long-legged velvet mites, parasitising gall midges (Cecidomyiidae) in about 100 million years old (Cretaceous) Kachin amber, Myanmar. In three of the four cases here reported, a single erythraeoidean mite was attached to a gall midge, while in one of the cases two mites are associated to a gall midge host. Of the reported gall midges, one specimen represents the ingroup Lestremiinae, two represent unnamed lineages closely related to Cecidomyiinae, and one specimen might represent the group Cecidomyiinae, being the earliest record of this group so far. In the extant fauna, there are no records of associations of erythraeoidean larvae with gall midges. After the Cretaceous, long-legged velvet mites may have shifted their host range, although knowledge on the host range of parasitengonan mites is still limited to arrive to definitive conclusion.

Keywords: Kachin amber, Burmese amber, Erythraeoidea, Cecidomyiidae, fossil parasites

Introduction

Parasites rule this world (Klompaker *et al.*, 2014). This includes parasites in the strict sense (*i.e.*, feeding on their hosts; Nelson *et al.*, 1975; Haug *et al.*, 2018; Gorb *et al.*, 2022), but also parasitoids (which ultimately kill their hosts; Hassel & Waage 1984; Kiesmüller *et al.*,

2022; Fei *et al.*, 2023) and complex aspects such as brood parasitism (Zink, 2000; Suhonen *et al.*, 2019; Sless *et al.*, 2023) or kleptoparasitism (Sivinski *et al.*, 1999; Shopido *et al.*, 2019, but see van der Wal *et al.*, 2021). Due to the overwhelming presence of all these life strategies (parasitism in the wide sense), we can assume that this has also been the case quite some time ago. Yet, the fossil record of parasitism is still very incomplete (De Baets & Littlewood, 2015; De Baets *et al.*, 2015, 2021), and recognising parasites as such is often challenging (Nagler *et al.*, 2017; Haug *et al.*, 2021; Schädel *et al.*, 2021). Identifying host-parasite interactions is often even more challenging (Castellani *et al.*, 2011; Klompaker *et al.*, 2014; van der Wal *et al.*, 2021).

Among the most frequently reported ectoparasitic organisms in amber are ticks and other mites (De Baets *et al.*, 2021). When considering parasitism in a wide sense (*sensu lato*), the record of mites as parasites goes back as far as the Carboniferous, as shown by the sedimentary fossil of an oribatidan mite (supposedly) phoretic on a grasshopper relative found in the Xiaheyan locality (*ca.* 320 mya, Robin *et al.*, 2016). Parasitic behaviour in a wide sense seems to already be quite frequent in mites in the Cretaceous given its extensive record as amber syninclusions from different deposits (*e.g.*, Magowski, 1995; Grimaldi, 2000; Delclòs *et al.*, 2007; Khaustov & Poinar, 2010; Arillo *et al.*, 2018; Konikiewicz & Małol, 2018). The first fossil records to be considered as representatives of parasitic behaviour of mites in a strict sense are in fact from the Early Cretaceous. These are Lebanese amber syninclusions (*ca.* 135–120 mya) in which larvae of parasitengonan mites are attached to dipteran hosts (Poinar *et al.*, 1994; Poinar & Milki, 2001; Azar, 2007; Azar *et al.*, 2010; Boucot & Poinar, 2010), and possibly feeding on them.

The mite group Parasitengona is an ingroup of Trombidiformes and characterised by a complex life cycle. The six-legged larva (see Haug 2020 for difficulties of the term) is parasitic on other euarthropodans and vertebrates (with very few exceptions (*e.g.*, Smith, 1998; Yoder *et al.*, 2012), while the deutonymph and adult are predatory, and the prelarva, protonymph and tritonymph are inactive (calyptostatic; Krantz & Walter, 2009). Among Parasitengona, Erythraeoidea is characterised by representatives with extremely long legs in their larval stage, hence the name long-legged velvet mites (Wohltmann *et al.*, 2006). The larvae of this group are parasitising a wide range of euarthropodan hosts (Welbourn, 1983; Wohltmann, 2000; Stroiński *et al.*, 2013; Bernard *et al.*, 2019; Haarder & Mąkol, 2022), among which flies (Diptera) are included. Flies also represent hosts for larvae of Erythraeoidea in the fossil record from a wide range of amber deposits (see Arillo *et al.*, 2018 and citations therein), including a wide range of ingroups of Diptera. In fact, the first records of parasitic mites (*sensu stricto*) are of erythraeoidean larvae parasitising biting midges (Ceratopogonidae, Poinar *et al.*, 1994; Poinar & Milki, 2001; Azar, 2007; Boucot & Poinar, 2010) and a non-biting midge (Chironomidae, Azar *et al.*, 2010). So far, there is only one report of a parasitic association between a gall midge of Cecidomyiidae and a possible long-legged velvet mite in Raritan New Jersey amber (94–89 mya) (Fig. 1A; Grimaldi, 2000). A gall midge as host for mites has also been reported in Baltic amber (35 mya), in this case an unidentified mite larva

(Fig. 1B; Eichmann, 2002), which is possibly a terrestrial representative of Parasitengona (*i.e.*, not a water mite). In extant fauna, there is only one report of a red velvet mite (Trombidiidae) larva, another parasitengonan ingroup, parasitising a gall midge (Thompson & Simmonds, 1965).

Cecidomyiidae has 25 species recorded from the Mesozoic (Jaschhof, 2021; Peñalver *et al.*, 2022), a relatively poor fossil record in relation to the richness of the extant fauna. For this reason, the most speciose ingroup, Cecidomyiinae, has not yet been recorded from that era, even though it was most probably already present by then (Dorchin *et al.*, 2019). The major lineages recorded from Mesozoic deposits are Catotrichinae, Lestremiinae, Micromyinae, “Porricondyliinae”, and “Winnertziinae” (Jaschhof, 2021). The last two are probably not valid names, due to non-monophyly in relation to Cecidomyiinae (Sikora *et al.*, 2019). Despite referred to by the vernacular name of gall midges, immatures of all the gall midges outside Cecidomyiinae are generally regarded as mycophagous and not gall-forming. Phytophagous and predatory species only appeared within Cecidomyiinae during the Cretaceous (Dorchin *et al.*, 2019).

Here we report for the first time cases of long-legged velvet mites (Erythraeoidea) parasitising gall midges (Cecidomyiidae) found in about 100 million-year-old (Cretaceous) Kachin amber, Myanmar. We discuss palaeontological and biological implications of these new findings.

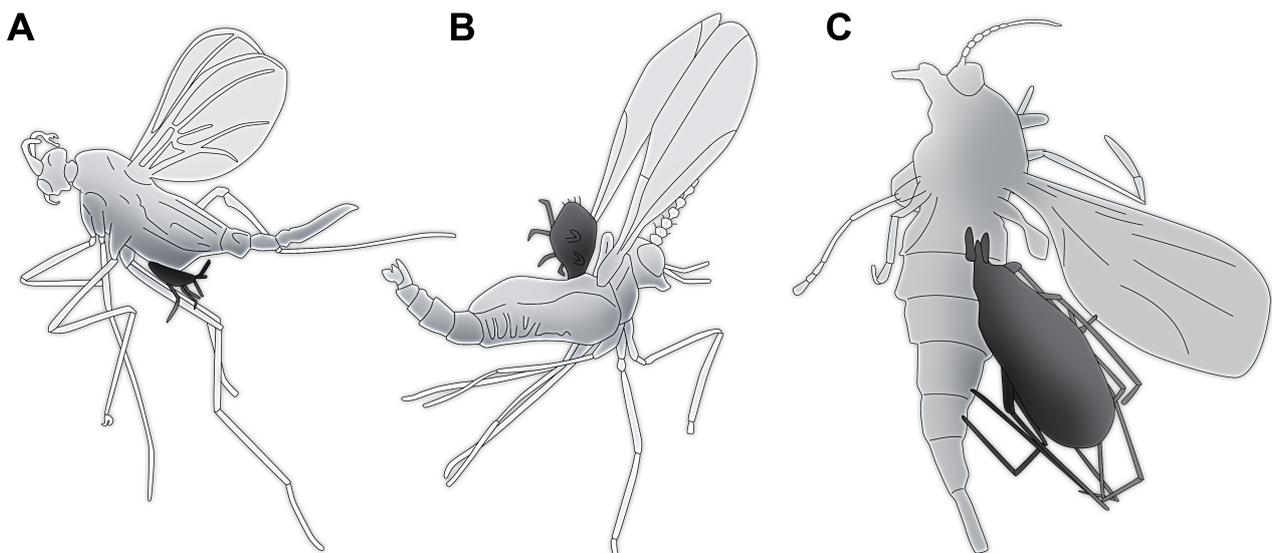


FIGURE 1. Some mites on flies in the fossil record from the literature. **A, B,** Mites of gall midges (Cecidomyiidae). **A,** From about 94–89 mya Raritan amber, New Jersey, USA (simplified from Grimaldi, 2000). **B,** From about 35 mya Baltic amber (simplified from Eichmann, 2002). **C,** Erythraeoidean mite on biting midge (Ceratopogonidae: *Leptoconops*) from about 100 mya Kachin amber, Myanmar (simplified from Konikiewicz & Mąkol, 2018).

Material and methods

Material

We documented four amber pieces with biosyninclusions in Kachin amber, Myanmar. Kachin amber has been dated to an age of about 100 million years (Cruickshank & Ko, 2003; Shi *et al.*, 2012; Yu *et al.*, 2019). The specimens were legally purchased on the trading platform ebay.com from the trader burmite-miner. Specimens are deposited in the Palaeo-Evo-Devo Research Group Collection of Arthropods, Ludwig-Maximilians-Universität München (LMU Munich), Germany, under repository numbers PED 3122, PED 3161, PED 3164, PED 3499. Additionally, we took the measurement of the longer axis of each amber piece.

Documentation methods

The specimens in amber were prepared with a drop of glycerol and a coverslip on top, to even the surface and reduce reflections. They were then photographed using an inverted digital microscope, Keyence VHX-6000. Images were produced from multiple stacks of adjacent frames and combined with the microscope built-in software. Either coaxial cross-polarised or ring illumination were used, depending on which retrieved a better contrast (Haug *et al.*, 2018). Accordingly, also the function HDR was used for improved sharpness and contrast (Haug *et al.*, 2013). The final figures were made using Photoshop CS2.

Literature data

Important depictions from the literature were simplified and redrawn using Adobe Illustrator CS2. This should allow the reader to compare the new findings to these already known ones.

Results

Description of amber piece PED 3122

General: The amber piece is 26 mm. Small midge (host) with mite attached to it (Fig. 2A). Other syninclusions present in the amber piece are two wasps, a prostigmatan mite and a dipteran insect.

Mite: Specimen preserved in ventral view. Body organised into gnathosoma and idiosoma; idiosoma with three pairs of legs, hence representing a larva. Gnathosoma attached to the dorsal side of the trunk of the host, between the posterior part of the thorax and anterior part of the abdomen, through anterior protruding structure (Fig. 2B). One pedipalp free, the other one in close proximity to its host. Four segments visible on the pedipalps. Thumb-like process of pedipalp not accessible. Urstigmata (structure

between coxae of two anterior legs) and anus absent. Shape of idiosoma indicates possible engorgement of host tissue. Length of idiosoma 0.46 mm, length of leg I 1.35 mm, leg II 1.13 mm, leg III 1.46 mm. First and second basipods (“coxae”) separated from each other.

Midge: Adult male, in lateral view. Ocelli seem absent (Fig. 2D). Antenna prominent, length of antenna 1.17 mm; antenna with 12 flagellomeres (Fig. 2D); each flagellomere with an elongate constriction, equally long as the thickened portion, the latter bearing several rows of simple setae (Fig. 2D). Maxillary palpus seemingly 3-segmented, about 0.7× the height of head (Fig. 2A). Wing length 1.17 mm; wing veins hard to distinguish, but at least C, R₁₊₂, Rs, R₄₊₅ and one Cu present; Rs apparently complete, near midlength; R₄₊₅ meeting C at distal part of wing (Fig. 2C). All legs missing tarsomeres distal to the first; first tarsomere very short, less than 0.2× the length of tibia on all legs (Fig. 2A). Genitalia indistinguishable.

Description of amber piece PED 3161

General: The amber piece is 15 mm. Small midge (host) with mite attached to it (Fig. 3A). A psocodean is also present in the amber piece.

Mite: Specimen preserved in dorsolateral position. Body organised into gnathosoma and idiosoma; idiosoma with three pairs of legs, hence representing a larva. Gnathosoma attached to the dorsal side of the abdomen of the host, between 3rd and 4th abdominal segment, through anterior protruding structure. One pedipalp visible. Thumb-like process of pedipalp and ventral side not accessible. Shape of idiosoma indicates possible engorgement of host tissue. Length of idiosoma 0.42 mm, length of leg I 0.32 mm.

Midge: Adult male in dorsolateral view (Fig. 3A). Ocelli indistinguishable. Antenna prominent, length of antenna 1.42 mm; antenna with 12 flagellomeres; each flagellomere with an elongate constriction, equally long as the thickened portion, the latter bearing several rows of simple setae. Maxillary palpus indistinguishable. Wings with only anterior portion visible; length of R₁₊₂ 1.23 mm; veins C, R₁₊₂, Rs, and R₅ distinguishable. Rs complete, situated near the apex of R₁₊₂. R₄₊₅ meeting C on anterior margin. Legs and genitalia mostly indistinguishable, but first tarsomere seems elongate (>0.3) in relation to the tibia.

Description of amber piece PED 3164

General: The amber piece is 37 mm. Small midge (host) with two mites attached to it (Fig. 3D). The piece had plant debris, but no other animal biosyninclusions were found.

Mite: Two mites. Body organised into gnathosoma and idiosoma; idiosoma of both specimens with three

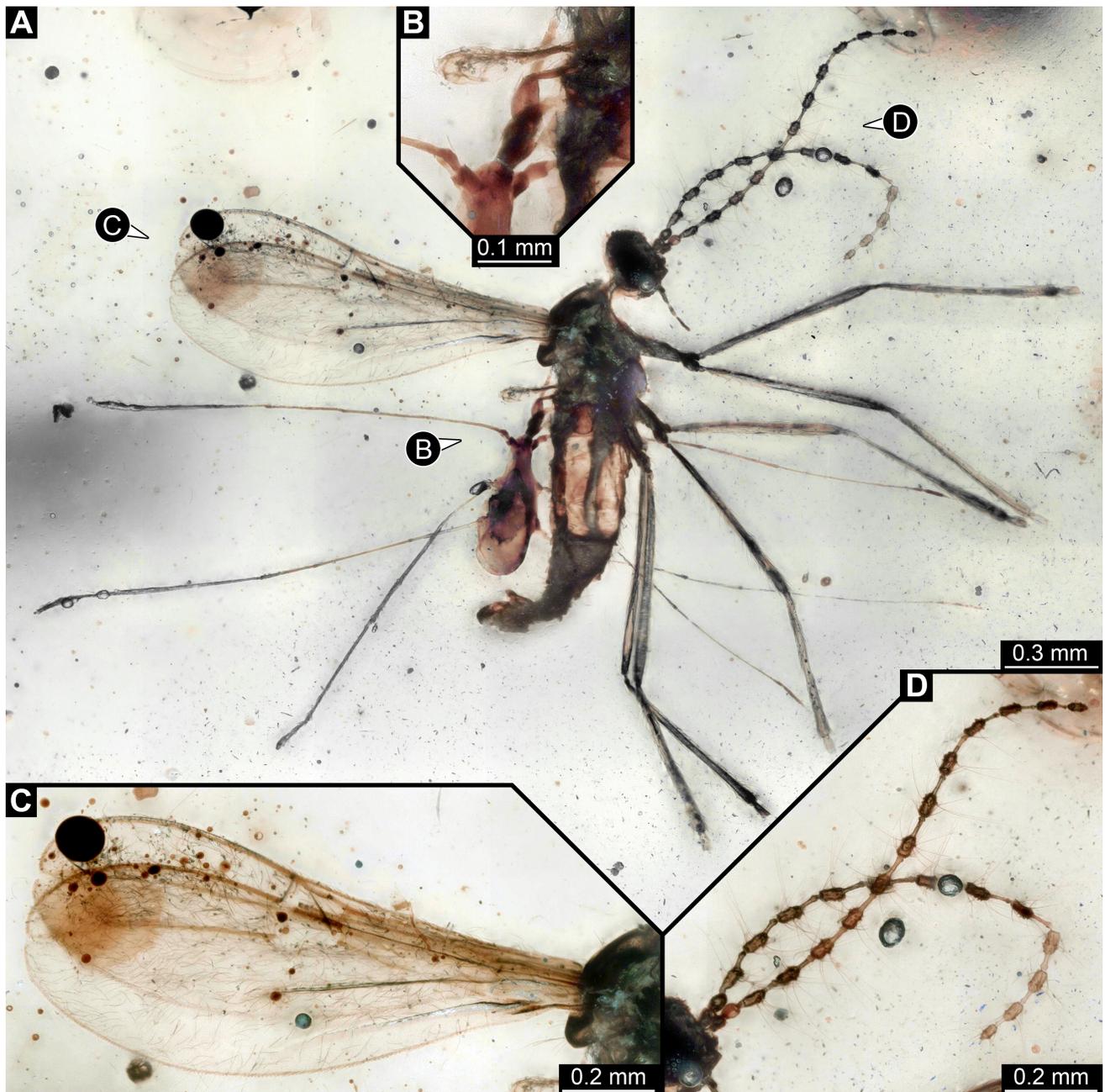


FIGURE 2. Fossil erythraeoidean mite on gall midge (Cecidomyiidae) from Kachin amber, Myanmar (PED 3122). **A**, Overview. **B**, Detail of the attachment point; note that the mite is only attached by its mouthparts, the long legs are not involved in attaching to the host. **C**, Close-up on the wings, showing gall-midge-type venation. **D**, Close-up on the gall-midge-type antennae.

pairs of legs, hence representing two larvae. Gnathosoma attached to the dorsal side of the trunk of the host through anterior protruding structure, one of the mites attached to the dorsal side of the anterior part of the thorax and the second one to the dorsal side of the anterior part of the abdomen. Shape of idiosoma indicates possible engorgement of host tissue. Of specimen on thorax, length of idiosoma 0.24 mm, length of leg III 0.40 mm, leg I and II inaccessible for measurements due to overlap with the midge head, thorax, and wing veins. Of specimen on abdomen, length of idiosoma 0.48 mm, length of leg III

1.04 mm, leg I and II inaccessible for measurements due to overlap with the wing veins of the midge.

Midge: Adult male in lateral view (Fig. 3D). Ocelli absent. Length of antenna 1.32 mm; antenna with 13 flagellomeres; each flagellomere with an elongate constriction, equally long as the thickened portion, the latter bearing several rows of simple setae. Maxillary palpus apparently 3-segmented, about 0.7× the height of head. Wing length 1.23 mm; wings with only anterior portion visible; veins C, R_{1+2} , Rs, R_{4+5} , and $M+r-m$, distinguishable; Rs situated near the base; R_{4+5} meeting C

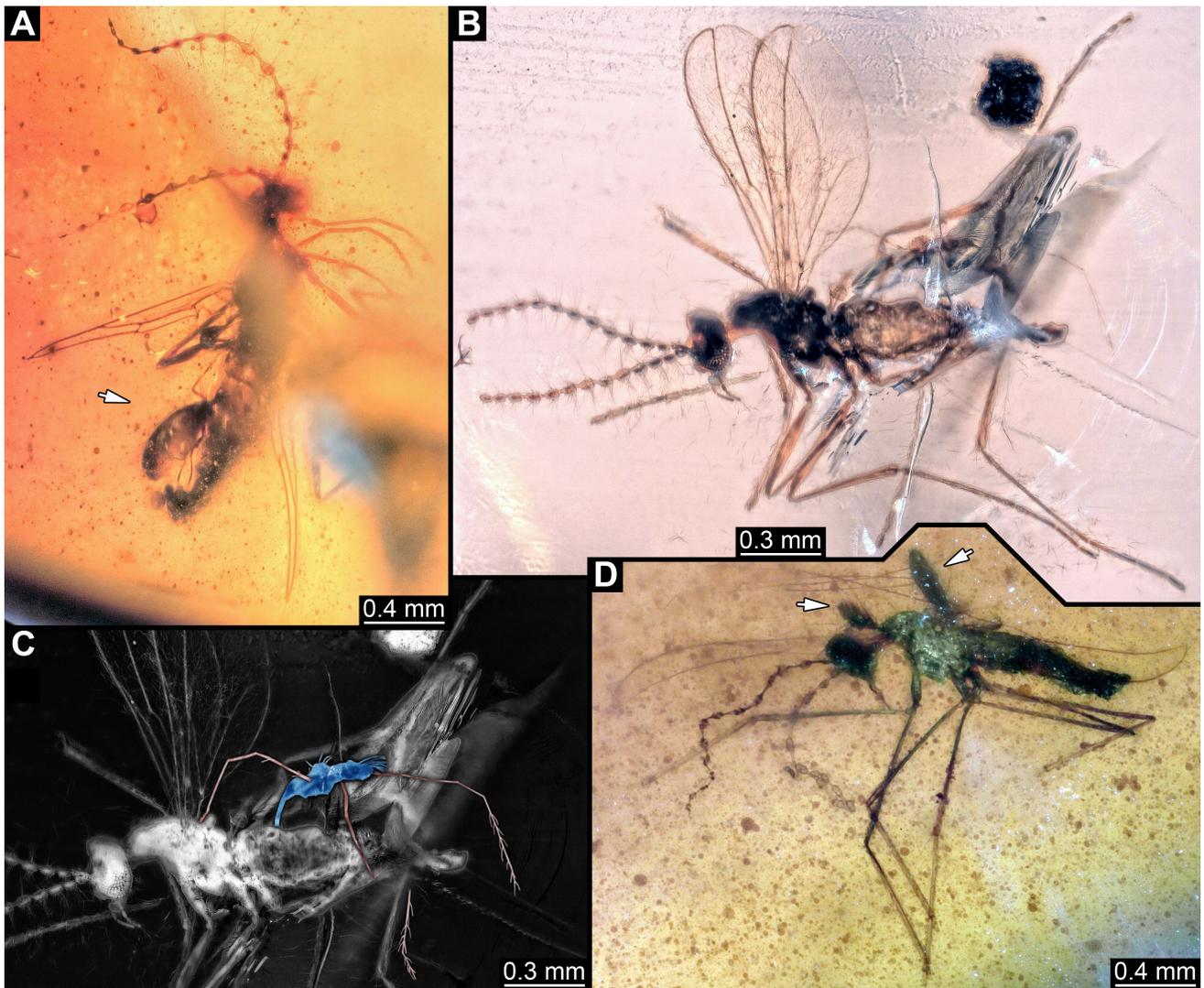


FIGURE 3. Fossil erythraoidean mites (arrows) on gall midges (Cecidomyiidae) from Kachin amber, Myanmar. **A**, PED 3161, overview (image flipped, arrow pointing to mite), Lestremiinae. **B**, **C**, PED 3499, Cecidomyiinae. **B**, Overview. **C**, Mite colour-marked. **D**, PED 3164, note that two mites are attached to this midge (arrows).

at the wing apex. All legs missing tarsomeres distal to the first; first tarsomere very short, less than $0.2\times$ the length of tibia on all legs. Genitalia indistinguishable.

Description of amber piece PED 3499

General: The amber piece is 19.9 mm. Small midge (host) with one mite attached to it (Fig. 3B, C). Other biosyninclusions in the amber piece are a beetle, a rake-legged mite, and three spiders.

Mite: Specimen preserved in dorsolateral position. Body organised into gnathosoma and idiosoma; idiosoma with three pairs of legs, hence representing a larva. Gnathosoma attached to the dorsal side of the anterior part of the abdomen of the host through anterior protruding structure. Due to the shape of idiosoma, it does not seem to be engorged of host tissue. Length of idiosoma 0.23 mm, length of leg I 0.63 mm, leg II 0.54 mm and leg III 0.78 mm.

Midge: Adult male in lateral view (Fig. 3B, C). Ocelli seem absent. Length of antenna 0.84 mm; antenna with 12 flagellomeres; each flagellomere with a short constriction, half as long as the thickened portion, the latter bearing several rows of simple setae. Maxillary palpus 3-segmented, about $0.62\times$ the height of head. Wing length 1.02 mm; wing veins C, R_{1+2} , Rs, R_{4+5} and one Cu present. Rs faint; R_{4+5} meeting C near the wing apex. Legs with tarsomeres attached; first tarsomere very short, less than $0.2\times$ the length of tibia on all legs, and about $0.15\times$ the length of second tarsomere. Genitalia indistinguishable.

Discussion

Identity of the specimens: the mites

Although many characteristics of the mites are concealed,

as is often the case for most mites embedded in amber, the general habitus and the leg length of at least twice the length of the idiosoma identify the mites in PED 3122, 3164 and 3499 as representatives of Erythraeoidea (Wohltmann *et al.*, 2006). As they only have three pairs of legs like in almost all larvae of mites, they are identified as larvae. The habitus of the mite in PED 3161 is compatible with erythraeoidean mites, although the legs are not as long as those of the remaining specimens reported here. Nevertheless, the apparent separation between the first two basipods found in this specimen leads to its identification as Erythraeoidea. The specimen in which most characters are visible (PED 3122; Fig. 2) demonstrates, besides the long legs, absence of urstigmata and anus, and the separation of the basipods. All these characters support the interpretation of the larvae as representatives of Erythraeoidea. Based on the difference of leg length, we assume the reported mite larvae belong to at least two different species.

Unfortunately, the ventral position of the mite in PED 3122 precludes the possibility of looking at further characters (or absence of them) on the dorsal side, such as the scutum (dorsal shield), eyes and idiosomal sensillae (bothriolae *sensu* Southcott, 1961). The non-accessibility of these structures prohibits a further-reaching phylogenetic interpretation of the mite larvae.

The large size of the mite specimen in PED 3122 compared to its host is not only a result of the engorgement of its idiosoma due to feeding on (possibly) the haemolymph of their host, but could also be linked to the process of neosomy that has been reported for other parasitengonan mites (secretion of new cuticle without relation to moulting; Małkol & Wohltmann, 2000; Wohltmann, 2000; Moniuszko & Małkol, 2016), although such phenomenon has yet to be confirmed for Erythraeoidea in particular.

Identity of the specimens: the midges

For the midges, *i.e.*, the hosts, more characters are available. The combination of long antennae with pedunculate flagellomeres (Figs 2D, 3A, B, D), the pattern of wing venation (Figs 2C, 3A, B, D), and the lack of tibial spurs, well visible in all the fossils, is unique to the group of gall midges, Cecidomyiidae (Gagné, 1981; Sikora *et al.*, 2019). Specimen PED 3161, with the vein C ending at the anterior margin of the wing (Fig. 3A) and a first tarsomere relatively elongate in relation to the tibia, is likely a representative of Lestremiinae (Gagné & Jaschhof, 2021).

The flagellomeres composed of an enlarged portion and a peduncle (uninodose flagellomere, as in Fig. 2D), lack of ocelli, long legs with a short first tarsomere (Figs 2A, 3B, D), indicate that PED 3164 and PED 3499 are likely representatives of a larger

unnamed ingroup of Cecidomyiidae (Jaschhof, 2000, 2021; Perkovsky & Fedotova, 2017; Fedotova *et al.*, 2022); this ingroup includes lineages traditionally considered “Porricondyliinae” and “Winnertziinae”, as well as Cecidomyiinae. According to the phylogeny proposed by Sikora *et al.* (2019), “Porricondyliinae” and “Winnertziinae” are non-monophyletic in relation to Cecidomyiinae, rendering them invalid. Specimens PED 3122 and PED 3164 lack the single apomorphic character of Cecidomyiinae (possible to be observed in these fossils), which is the number of flagellomeres different from 14. In combination, these characters allow to restrict the area of the tree for these two specimens to being outside Cecidomyiinae, but still within the larger unnamed group outlined above.

Specimen in PED 3499 has an antenna with 12 flagellomeres, which is generally considered an autapomorphy of Cecidomyiinae. Additionally, a faint vein Rs is diagnostic of Cecidomyiinae. The specimen may represent the first record of Cecidomyiinae during the Mesozoic.

In gall midges outside Cecidomyiinae (here represented by PED 3122, 3161 and 3164), the larvae are generally considered mycophagous, which is the ancestral feeding mode in Cecidomyiidae (Dorchin *et al.*, 2019). More precisely, the larvae are associated with fungi growing under tree bark and in forest litter (Penttinen & Spungis, 2007; Fedotova *et al.*, 2022), the same habitat as for erythraeoidean mite larvae (Wohltmann, 2000). This could explain their encounter with the parasites. Moreover, the proximity with trees also facilitates the entrapment in amber. The specimen in PED 3499, seemingly representing the lineage in which predatory and gall-forming larvae arose, may have had a different diet than mycophagy, but that is still uncertain given the lack of information about immature gall midges from the Mesozoic.

Interaction

The interaction of the fossils, with the mites being in contact with the midges by their anterior protruding structures, most likely representing the mouthparts, clearly indicates that it is a parasitic one. The overall posture of the fossil mites resembles that known from modern parasitic ones (*e.g.*, Southcott, 1992: fig 13; Baker & Selden, 1997: figs 9, 10; Goldarazena *et al.*, 1999: figs 1, 2; Małkol *et al.*, 2010: fig. 1; Haarder & Małkol, 2022: fig. 1A, B; Mayoral *et al.*, 2023: fig. 1). Together with the relationship (as representatives of Erythraeoidea), it clearly provides strong indication that the mites parasitised on the midges.

Parasitism by long-legged velvet mites on dipterans

The syninclusions here reported are considered the

oldest report of long-legged velvet mites parasitising gall midges in the fossil record, since Kachin Myanmar amber is considered to be 100 million years of age. This is close in age to, but still older than, the Grimaldi (2000) report from New Jersey amber, both being Cretaceous, although not close geographically. Therefore, the association of gall midges and long-legged velvet mites seems to have been widespread in Cretaceous times, at least in the Kachin amber forest.

Erythraeoidean mites parasitise a wide range of hosts, and host specificity appears to vary between lineages (Southcott, 1992; Wohltmann, 2000). The consistency of the cases described here shows that the association between gall midges and erythraeoidean mites was probably not accidental. To the best of our knowledge, there is no record of gall midges being parasitised by long-legged velvet mites in the extant fauna. The larvae that produce galls in plants are representatives of Cecidomyiinae and are considered detrimental for crops (Harris *et al.*, 2003; Stuart *et al.*, 2012; McMechan *et al.*, 2021). Due to this economic importance, gall midges of the group Cecidomyiinae and their biological associations have been widely studied. Even an ingroup of terrestrial mites of Parasitengona, *Balaustium*, has been proposed as a possible biological control method of their larval population through predation (Muñoz-Cárdenas *et al.*, 2015). Nevertheless, we still lack knowledge on all other gall midge groups and their possible interactions with parasites. On the other hand, it has been estimated that hosts are still unknown for more than 20% of terrestrial mites of the group Parasitengona (Małkol *et al.*, 2012).

Parasitism on “flying insects” (most of them do in fact not fly) is generally considered an autapomorphy for Parasitengona (Söller *et al.*, 2001). In the extant fauna, Diptera is only one of the many groups long-legged velvet mites (Erythraeoidea) have been found parasitising (Welbourn, 1983; Wohltmann, 2000; Stroński *et al.*, 2013; Bernard *et al.*, 2019; Haarder & Małkol, 2022). Nevertheless, fossil representatives of Erythraeoidea have mainly been reported in association with dipterans (see Arillo *et al.*, 2018; Konikiewicz & Małkol, 2018), and reports of them parasitising other groups of Euarthropoda is scarce (a moth in Poinar *et al.*, 1991; a spider in Weitschat & Wichard, 1998, and a booklouse, also in Weitschat & Wichard, 1998). For this aspect, we have to consider that amber represents an imperfect sampling method (De Baets *et al.*, 2021), and it should not be disregarded that the chances of finding associations between erythraeoideans and dipterans being more common than to any other euarthropodan may be the result of this bias in the fossil record. What the resin has caught while still fresh depends on the resin-producing tree, the height where the resin was produced, and the behaviour and size of the organisms, among other factors (Solórzano-Kraemer *et al.*, 2015).

Moreover, what is later found in amber is also affected by the possibilities of the tissues of the organism being preserved over time (De Baets *et al.*, 2021). Resin tends to entrap small flying insects close to the tree bark on the trunk region of the tree (Solórzano-Kraemer *et al.*, 2015, 2018), therefore not accurately representing the entire diversity of Euarthropoda. In consequence, dipterans are likely overrepresented in amber, leading to a higher chance of an overrepresentation of dipteran parasitic relationships as well.

Yet, even accounting for a possible bias in the fossil record, it is astonishing that the present report is not the first parasitic association between dipteran hosts and long-legged velvet mites that seem to have gone extinct. Poinar *et al.* (1997) also reported the presence of a long-legged velvet mite larva parasitising a non-biting midge (Chironomidae) in Canadian Cretaceous amber (79 mya). Also, this parasite-host relationship has possibly been lost in time, since there is no present counterpart of such association. Konikiewicz & Małkol (2018) have also pointed out that biting midges (Ceratopogonidae) are now considered rare hosts for erythraeoidean larvae, but this association may have been much more frequent in the past based on the fossil record (see also Fig. 1C).

In many extant representatives, long-legged velvet mites are highly resistant to dryness, compared to the other terrestrial representatives of Parasitengona (Wohltmann, 2000). This seems to have been different in the past. Therefore, a possible shift from more moist-preferring hosts to more dry-preferring ones, linked to their ability to occupy drier environments, should have occurred after the Cretaceous due to novel host associations (Konikiewicz & Małkol, 2018). Since throughout the larval stage the host not only serves as an energy source for Parasitengona, but also for dispersion (Treat, 1975; Seeman & Walter, 2023), the change to new hosts should also have enabled dispersal to new habitats.

For a parasitic relationship between two groups, the first filter is the possibility of an encounter between them (Combes, 1991). Although knowledge concerning the environment larvae of Erythraeoidea inhabit before attaching to their hosts is limited, in general, extant representatives of long-legged velvet mites are associated to litter and tree bark (Wohltmann, 2000, 2001). Larvae of gall midges represented in the present study likely inhabited under tree bark and forest litter, where erythraeoidean mites could find the adults in copula or the ovipositing females. It could be the case that extant representatives of Cecidomyiidae do not share the same biotope with erythraeoidean mites, and the probability of an encounter between these two groups is lower than in the past, leading to lack of reports of parasitism in the present fauna and crop environments. Much is still to unravel about the evolution of parasitic associations in

Parasitengona, in particular with respect to host availability in the microhabitats occupied by mite larvae. However, the present study reveals that the fact that much is yet to explore concerning current ecological associations between mites and their hosts makes interpreting the fossil record a challenging task.

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References

- Azar, D. (2007) Preservation and accumulation of biological inclusions in Lebanese amber and their significance. *Comptes Rendus Palevol*, 6 (1–2), 151–156.
<https://doi.org/10.1016/j.crpv.2006.10.004>
- Azar, D., Gèze, R. & Acra, F. (2010) Lebanese amber. In: Penney, D. (Ed.), *Biodiversity of fossils in amber from the major world deposits*. Siri Scientific Press, Manchester, pp. 271–298.
- Arillo, A., Blagoderov, V. & Peñalver, E. (2018) Early Cretaceous parasitism in amber: A new species of *Burmazelmira* fly (Diptera: Archizelmiridae) parasitized by a *Leptus* sp. mite (Acari, Erythraeidae). *Cretaceous Research*, 86, 24–32.
<https://doi.org/10.1016/j.cretres.2018.02.006>
- Baker, A.S. & Selden, P.A. (1997) New morphological and host data for the ectoparasitic larva of *Leptus hidakai* Kawashima (Acari, Acariformes, Erythraeidae). *Systematic Parasitology*, 36, 183–191.
<https://doi.org/10.1023/A:1005757014689>
- Bernard, R., Felska, M. & Małol, J. (2019) Erythraeid larvae parasitizing dragonflies in Zambia—description of *Leptus (Leptus) chingombensis* sp. nov. with data on biology and ecology of host-parasite interactions. *Systematic and Applied Acarology*, 24 (5), 790–813.
<https://doi.org/10.11158/saa.24.5.6>
- Boucot, A.J. & Poinar, G.O. (2010) *Fossil behavior compendium*. CRC Press, Boca Raton, Florida, 363 pp.
<https://doi.org/10.1201/9781439810590>
- Castellani, C., Maas, A., Waloszek, D. & Haug, J.T. (2011) New pentastomids from the Late Cambrian of Sweden—deeper insight of the ontogeny of fossil tongue worms. *Palaeontographica A*, 293 (4–6), 95–145.
<https://doi.org/10.1127/pala/293/2011/95>
- Combes, C. (1991) Ethological aspects of parasite transmission. *The American Naturalist*, 138 (4), 866–880.
<https://doi.org/10.1086/285257>
- Cruickshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, 21, 441–455.
[https://doi.org/10.1016/S1367-9120\(02\)00044-5](https://doi.org/10.1016/S1367-9120(02)00044-5)
- De Baets, K., Dentzien-Dias, P., Upeniece, I., Verneau, O. & Donoghue, P.C. (2015) Constraining the deep origin of parasitic flatworms and host-interactions with fossil evidence. *Advances in Parasitology*, 90, 93–135.
<https://doi.org/10.1016/bs.apar.2015.06.002>
- De Baets, K., Huntley, J., Klompaker, A., Schiffbauer, J. & Muscente, A. (2021) The fossil record of parasitism: its extent and taphonomic constraints. In: De Baets, K. & Huntley, J.W. (Eds), *The evolution and fossil record of parasitism: coevolution and paleoparasitological techniques*. Topics in Geobiology 50, Springer, Cham, pp. 1–50.
https://doi.org/10.1007/978-3-030-52233-9_1
- De Baets, K. & Littlewood, D.T.J. (2015) The importance of fossils in understanding the evolution of parasites and their vectors. *Advances in Parasitology*, 90, 1–51.
<https://doi.org/10.1016/bs.apar.2015.07.001>
- Delclòs, X., Arillo, A., Peñalver, E., Barrón, E., Soriano, C., Valle, R.L.D., Bernárdez, E., Corral, C. & Ortuño, V.M. (2007) Fossiliferous amber deposits from the Cretaceous (Albian) of Spain. *Comptes Rendus Palevol*, 6 (1–2), 135–149.
<https://doi.org/10.1016/j.crpv.2006.09.003>
- Dorchin, N., Harris, K.M. & Stireman J.O. (2019) Phylogeny of the gall midges (Diptera, Cecidomyiidae, Cecidomyiinae): Systematics, evolution of feeding modes and diversification rates. *Molecular Phylogenetics and Evolution*, 140, 106602.
<https://doi.org/10.1016/j.ympev.2019.106602>
- Eichmann, F. (2002) Paläosymbiosen im Bernstein. *Arbeitskreis Paläontologie Hannover*, 30 (1), 1–28.
- Fedotova, Z.A., Perkovsky, E.E., Ross, A.J. & Zhang, Q. (2022) A new genus and species of gall midges the tribe Winnertziini (Diptera, Cecidomyiidae, Porricondylinae) from lower Eocene Fushun amber from China. *Palaeoentomology*, 5 (1), 90–98.
<https://doi.org/10.11646/palaeoentomology.5.1.11>
- Fei, M., Gols, R. & Harvey, J.A. (2023) The biology and ecology of parasitoid wasps of predatory arthropods. *Annual Review of Entomology*, 68, 109–128.
<https://doi.org/10.1146/annurev-ento-120120-111607>
- Gagné, R.J. (1981) Cecidomyiidae. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (coordinators), *Manual of Nearctic Diptera*. Volume I. Agriculture Canada, Ottawa, pp. 489–492.
- Gagné, R.J. & Jaschhof, M. (2021) *A catalog of the Cecidomyiidae (Diptera) of the world*. Fifth edition. Digital, Washington, D.C., 816 pp.
- Goldarazena, A., Jordana, R. & Zhang, Z.Q. (1999) Notes on *Abrolophus neobrevicollis* Z. and G. and *Grandjeanella multisetosa* Z. and G. (Acari: Erythraeidae) with the seasonal abundance in Mediterranean Spain. *International Journal of Acarology*, 25 (1), 29–36.
<https://doi.org/10.1080/01647959908683609>
- Gorb, S.N., Wildermuth, H., Kohl, S. & Büsse, S. (2022) Tarsal

- attachment structures of the biting midge *Forcipomyia paludis* (Diptera: Ceratopogonidae), a specialized ectoparasite of Odonata imagines. *Zoomorphology*, 141 (3–4), 297–306.
<https://doi.org/10.1007/s00435-022-00561-9>
- Grimaldi, D. (2000) *Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey*. Backhuys Publishers, Leiden, 498 pp.
- Haarder, S. & Mąkol, J. (2022) Terrestrial Parasitengona mites (Trombidiformes) of Denmark—new data on parasite-host associations and new country records. *Acarologia*, 62 (2), 508–520.
<https://doi.org/10.24349/yglc-mnck>
- Harris, M.O., Stuart, J.J., Mohan, M., Nair, S., Lamb, R.J. & Rohfritsch, O. (2003) Grasses and gall midges: plant defense and insect adaptation. *Annual Review of Entomology*, 48, 549–577.
<https://doi.org/10.1146/annurev.ento.48.091801.112559>
- Hassell, M.P. & Waage, J.K. (1984) Host-parasitoid population interactions. *Annual Review of Entomology*, 29 (1), 89–114.
<https://doi.org/10.1146/annurev.en.29.010184.000513>
- Haug, C., Shannon, K.R., Nyborg, T. & Vega, F.J. (2013) Isolated mantis shrimp dactyli from the Pliocene of North Carolina and their bearing on the history of Stomatopoda. *Boletín de la Sociedad Geológica Mexicana*, 65 (2), 273–284.
<https://doi.org/10.18268/BSGM2013v65n2a9>
- Haug, J.T. (2020) Why the term “larva” is ambiguous, or what makes a larva? *Acta Zoologica*, 101, 167–188.
<https://doi.org/10.1111/azo.12283>
- Haug, J.T., Haug, C. & Nagler, C. (2021) Evolutionary history of crustaceans as parasites. In: De Baets, K. & Huntley, J. W. (Eds), *The Evolution and Fossil Record of Parasitism*. Topics in Geobiology 49. Springer, Cham, pp. 347–376.
https://doi.org/10.1007/978-3-030-42484-8_10
- Haug, J.T., Müller, P. & Haug, C. (2018) The ride of the parasite: a 100-million-year old mantis lacewing larva captured while mounting its spider host. *Zoological Letters*, 4, 31.
<https://doi.org/10.1186/s40851-018-0116-9>
- Jaschhof, M. (2000) Catotrichinae subfam. n.: a re-examination of higher classification in gall midges (Diptera: Cecidomyiidae). *Entomological Science*, 3 (4), 639–652
- Jaschhof, M. (2021) A review of gall midges (Diptera: Cecidomyiidae) described from Mesozoic deposits. *Palaeoentomology*, 4 (1), 1–14.
<https://doi.org/10.11646/palaeoentomology.4.1.1>
- Khaustov, A.A. & Poinar, G. (2011) *Protoresinacarus brevipedis* gen. n., sp. n. from Early Cretaceous Burmese amber: the first fossil record of mites of the Family Resinacaridae (Acari: Heterostigmata: Pyemotoidea). *Historical Biology*, 23 (2–3), 219–222.
<https://doi.org/10.1080/08912963.2010.508881>
- Kiesmüller, C., Haug, J.T., Müller, P. & Hörnig, M.K. (2022) A case of frozen behaviour: A flat wasp female with a beetle larva in its grasp in 100-million-year-old amber. *Fossil Record*, 25, 287–305.
<https://doi.org/10.3897/fr.25.82469>
- Klompaker, A.A., Artal, P., van Bakel, B.W., Fraaije, R.H. & Jagt, J.W. (2014) Parasites in the fossil record: a Cretaceous fauna with isopod-infested decapod crustaceans, infestation patterns through time, and a new ichnotaxon. *PLoS One*, 9 (3), e92551.
<https://doi.org/10.1371/journal.pone.0092551>
- Konikiewicz, M. & Mąkol, J. (2018) Insight into fossil fauna of terrestrial Parasitengona mites (Trombidiformes: Prostigmata)—The first representatives of Erythraeina Welbourn, 1991 and Trombidiina Welbourn, 1991 in Burmese amber. *Cretaceous Research*, 89, 60–74.
<https://doi.org/10.1016/j.cretres.2018.02.017>
- Krantz, G.W. & Walter, D.E. (2009) *A manual of acarology*. 3rd edn. Texas Tech University Press, Lubbock, 807 pp.
- Magowski, W.L. (1995) Fossil heterostigmatid mites in amber—85 million year-old arthropod mite relationships. In: Kropczyńska, D., Boczek, J. & Tomczyk, A. (Eds), *The Acari. Physiological and Ecological Aspects of Acari-Host Relationships*. Proceedings of the 2nd International Meeting of EURAAC, DABOR Publ. House, Krynica, pp. 53–58.
- Mąkol, J., Felska, M., Moniuszko, H. & Zalesny, G. (2012) Redescription of *Leptus kattikus* Haitlinger, 2009 (Actinotrichida, Parasitengona, Erythraeidae) and molecular identification of its host from DNA barcoding. *Zootaxa*, 3569 (1), 67–78.
<https://doi.org/10.11646/zootaxa.3569.1.5>
- Mąkol, J., Łaydanowicz, J. & Kłosiska, A. (2010) Myrmecophilous Parasitengona (Acari: Prostigmata)—accident or adaptation? *Annales Zoologici*, 60 (3), 429–437.
<https://doi.org/10.3161/000345410X535415>
- Mąkol, J. & Wohltmann, A. (2000) A redescription of *Trombidium holosericeum* (Linnaeus, 1758) (Acari: Actinotrichida: Trombidioidea) with characteristics of all active instars and notes on taxonomy and biology. *Annales Zoologici*, 50 (1), 67–91.
- Mayoral, J., Miralles-Núñez, A., Sánchez, J. & Espadaler, X. (2023) Parasitic mites of the genus *Forania* (Acari, Erythraeidae) on ants (Hymenoptera: Formicidae) in NE Spain: When taxonomy meets citizen science. *Systematic and Applied Acarology*, 28 (1), 123–130.
<https://doi.org/10.11158/saa.28.1.11>
- McMechan, A.J., Hodgson, E.W., Varenhorst, A.J., Hunt, T., Wright, R. & Potter, B. (2021) Soybean gall midge (Diptera: Cecidomyiidae), a new species causing injury to soybean in the United States. *Journal of Integrated Pest Management*, 12, 8.
<https://doi.org/10.1093/jipm/pmab001>
- Moniuszko, H. & Mąkol, J. (2016) Host-parasite association in trombiculid mites (Actinotrichida: Trombiculidae) of temperate zone—the case of *Hirsutiella zachvatkini* (Schluger, 1948); are we dealing with prolonged contact with the host? *Parasites & Vectors*, 9, 61.
<https://doi.org/10.1186/s13071-016-1339-2>
- Muñoz-Cárdenas, K., Fuentes-Quintero, L.S., Rueda-Ramírez, D.,

- Rodríguez, C.D. & Cantor, R.F. (2015) The Erythraeoidea (Trombidiformes: Prostigmata) as biological control agents, with special reference to the genus *Balaustium*. In: Carrillo, D., de Moraes, G. J. & Peña, J. E. (Eds), *Prospects for biological control of plant feeding mites and other harmful organisms*. Progress in Biological Control 19, Springer, Cham, pp. 207–239.
https://doi.org/10.1007/978-3-319-15042-0_8
- Nagler, C., Hyžný, M. & Haug, J.T. (2017) 168 million years old “marine lice” and the evolution of parasitism within isopods. *BMC Evolutionary Biology*, 17, 76.
<https://doi.org/10.1186/s12862-017-0915-1>
- Nelson, W.A., Keirans, J.E., Bell, J.F. & Clifford, C.M. (1975) Host-ectoparasite relationships. *Journal of Medical Entomology*, 12 (2), 143–166.
<https://doi.org/10.1093/jmedent/12.2.143>
- Peñalver, E., Arillo, A. & Nel, A. (2022) A review of the Cretaceous genus *Eltxo* (Diptera: Cecidomyiidae) with description of the new species *Eltxo grimaldii* from El Soplao amber. *Palaeoentomology*, 5 (5), 461–467.
<https://doi.org/10.11646/palaeoentomology.5.5.7>
- Penttinen, J. & Spungis, V. (2007) Additions to the Finnish fauna of log midges (Diptera, Cecidomyiidae: Porricondylinae). *Sahlbergia*, 12 (1), 36–42.
- Perkovsky, E.E. & Fedotova, Z.A. (2017) The second Cretaceous gall midge genus of the tribe Diallactiini (Diptera, Cecidomyiidae) from the Late Cretaceous Burmese amber. *Vestnik Zoologii*, 51 (2), 117–124.
<https://doi.org/10.1515/vzoo-2017-0017>
- Poinar, G.O., Jr., Treat, A.E. & Southcott, R.V. (1991) Mite parasitism of moths: Examples of paleosymbiosis in Dominican amber. *Experientia*, 47 (2), 210–212.
<https://doi.org/10.1007/BF01945430>
- Poinar, G.O., Jr., Acra, A. & Acra, F. (1994) Animal-animal parasitism in Lebanese amber. *Medical Science Research*, 22 (2), 159.
- Poinar, G.O. Jr., Krantz, G.W., Boucot, A.J. & Pike, T.M. (1997) A unique Mesozoic parasitic association. *Naturwissenschaften*, 84 (7), 321–322.
<https://doi.org/10.1007/s001140050405>
- Poinar, G.O., Jr. & Milki, R. (2001) *Lebanese amber. The oldest insect ecosystem in fossilized amber*. Oregon State University Press, Corvallis, Oregon, 96 pp.
- Robin, N., Béthoux, O., Sidorchuk, E., Cui, Y.Y., Li, Y.N., Germain, D., King, A., Berenguer, F. & Ren, D. (2016) A carboniferous mite on an insect reveals the antiquity of an inconspicuous interaction. *Current Biology*, 26 (10), 1376–1382.
<https://doi.org/10.1016/j.cub.2016.03.068>
- Schädel, M., Hörnig, M. K., Hyžný, M. & Haug, J.T. (2021) Mass occurrence of small isopodan crustaceans in 100-million-year-old amber: an extraordinary view on behaviour of extinct organisms. *PalZ*, 95, 429–445.
<https://doi.org/10.1007/s12542-021-00564-9>
- Seeman, O.D. & Walter, D.E. (2023) Phoresy and mites: more than just a free ride. *Annual Review of Entomology*, 68 (1), 69–88.
<https://doi.org/10.1146/annurev-ento-120220-013329>
- Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L. & Li, X.H. (2012) Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, 37, 155–163.
<https://doi.org/10.1016/j.cretres.2012.03.014>
- Shodipo, M.O., Gomez, R.D.C., Welicky, R.L. & Sikkel, P.C. (2019) Apparent kleptoparasitism in fish—parasitic gnathiid isopods. *Parasitology Research*, 118, 653–655.
<https://doi.org/10.1007/s00436-018-6152-8>
- Sikora, T., Jaschhof, M., Mantič, M., Kaspřák, D. & Ševčík, J. (2019) Considerable congruence, enlightening conflict: molecular analysis largely supports morphology-based hypotheses on Cecidomyiidae (Diptera) phylogeny. *Zoological Journal of the Linnean Society*, 185 (1), 98–110.
<https://doi.org/10.1093/zoolinnean/zly029>
- Sivinski, J., Marshall, S. & Petersson, E. (1999) Kleptoparasitism and phoresy in the Diptera. *Florida Entomologist*, 82, 179–197.
- Sless, T.J., Danforth, B.N. & Searle, J.B. (2023) Evolutionary origins and patterns of diversification in animal brood parasitism. *The American Naturalist*, 202 (2), 107–121.
<https://doi.org/10.1086/724839>
- Smith, B.P. (1998) Loss of larval parasitism in parasitengonine mites. *Experimental & Applied Acarology*, 22, 187–199.
<https://doi.org/10.1023/A:1006010230247>
- Söller, R., Wohltmann, A., Witte, H. & Blohm, D. (2001) Phylogenetic relationships within terrestrial mites (Acari: Prostigmata, Parasitengona) inferred from comparative DNA sequence analysis of the mitochondrial cytochrome oxidase subunit I gene. *Molecular Phylogenetics and Evolution*, 18 (1), 47–53.
<https://doi.org/10.1006/mpev.2000.0855>
- Solórzano-Kraemer, M.M., Delclòs, X., Clapham, M.E., Arillo, A., Peris, D., Jäger, P., Stebner, F. & Peñalver, E. (2018) Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. *Proceedings of the National Academy of Sciences*, 115 (26), 6739–6744.
<https://doi.org/10.1073/pnas.1802138115>
- Solórzano-Kraemer, M.M., Kraemer, A.S., Stebner, F., Bickel, D.J. & Rust, J. (2015) Entrapment bias of arthropods in Miocene amber revealed by trapping experiments in a tropical forest in Chiapas, Mexico. *PLoS One*, 10 (3), e0118820.
<https://doi.org/10.1371/journal.pone.0118820>
- Southcott, R.V. (1961) Studies on the systematics and biology of the Erythraeoidea (Acarina), with critical revision of the genera and subfamilies. *Australian Journal of Zoology*, 9 (3), 367–610.
<https://doi.org/10.1071/ZO9610367>
- Southcott, R.V. (1992) Revision of the larvae of *Leptus* Latreille (Acarina: Erythraeidae) of Europe and North America, with descriptions of post-larval instars. *Zoological Journal of the Linnean Society*, 105 (1), 1–153.
<https://doi.org/10.1111/j.1096-3642.1992.tb01228.x>

- Stroiński, A., Felska, M. & Małkol, J. (2013) A review of host-parasite associations between terrestrial parasitengona (Actinotrichida: Prostigmata) and bugs (Hemiptera). *Annales Zoologici*, 63 (2), 195–221.
<https://doi.org/10.3161/000345413X669522>
- Stuart, J.J., Chen, M.S., Shukle, R. & Harris, M.O. (2012) Gall midges (Hessian flies) as plant pathogens. *Annual Review of Phytopathology*, 50, 339–357.
<https://doi.org/10.1146/annurev-phyto-072910-095255>
- Suhonen, J., Ilvonen, J.J., Nyman, T. & Sorvari, J. (2019) Brood parasitism in eusocial insects (Hymenoptera): role of host geographical range size and phylogeny. *Philosophical Transactions of the Royal Society B*, 374 (1769), 20180203.
<https://doi.org/10.1098/rstb.2018.0203>
- Thompson, W.R. & Simmonds, F.J. (1965) *A catalogue of the parasites and predators of insect pests*. Section 4. Host Predator Catalogue. Commonwealth Agricultural Bureaux, Wallingford, UK, 208 pp.
- Treat, A.E. (1975) *Mites of moths and butterflies*. Cornell University Press Ithaca, New York, 362 pp.
- van der Wal, S., Schädel, M., Ekrt, B. & Haug, J.T. (2021) Description and ontogeny of a 40-million-year-old parasitic isopodan crustacean: *Parvucymoides dvorakorum* gen. et sp. nov. *PeerJ*, 9, e12317.
<https://doi.org/10.7717/peerj.12317>
- Weitschat, W. & Wichard, W. (1998) *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Dr. Friedrich Pfeil, München, 256 pp.
- Welbourn, W.C. (1983) Potential use of trombidoid and erythraeid mites as biological control agents of insect pests. In: Hoy, M.A., Cunningham, G.L. & Knutson, L. (Eds), *Biological control of pests by mites*. Agricultural Experiment Station, Division of Agriculture and Natural Resources, Special Publication 3304, University of California, Berkeley, pp. 103–140.
- Wohltmann, A. (2000) The evolution of life histories in Parasitengona (Acari: Prostigmata). *Acarologia*, 41 (1–2), 145–204.
- Wohltmann, A. (2001) Closely related species of Parasitengonae (Acari: Prostigmata) inhabiting the same area: Patterns facilitating coexistence. In: Halliday, R.B., Walter, D.E., Proctor, H.C., Norton, R.A. & Colloff, M.J. (Eds), *Proceedings of the 10th International Congress of Acarology*. CSIRO Publishing, Melbourne, pp. 121–135.
- Wohltmann, A., Gabryś, G. & Małkol, J. (2006) Acari: Terrestrial Parasitengona inhabiting transient biotopes. In: Gerecke, R. (Ed.), *Süßwasserfauna von Mitteleuropa*, Vol. 7/2–1 Chelicerata: Araneae/Acari I (Vol. 7). Springer Spektrum, Berlin, pp. 158–240.
<https://doi.org/10.1007/978-3-662-55958-1>
- Yoder, A., Jajack A. J., Tomko, P.M., Rosselot, A.E., Gribbins, K.M. & Benoit, J.B. (2012) Pollen feeding in *Balaustium murorum* (Acari: Erythraeidae): visualization and behaviour. *International Journal of Acarology*, 38, 641–647.
<https://doi.org/10.1080/01647954.2012.733024>
- Yu, T.T., Kelly, R., Mu, L., Ross, A., Kennedy, J., Broly, P., Xia, F.Y., Zhang, H.C., Wang, B. & Dilcher, D. (2019) An ammonite trapped in Burmese amber. *Proceedings of the National Academy of Sciences*, 116, 11345–11350.
<https://doi.org/10.1073/pnas.1821292116>
- Zink, A.G. (2000) The evolution of intraspecific brood parasitism in birds and insects. *The American Naturalist*, 155 (3), 395–405.
<https://doi.org/10.1086/303325>