



<https://doi.org/10.11646/palaeoentomology.7.4.3>

<https://zoobank.org/urn:lsid:zoobank.org:pub:DB769B9A-F756-4108-A900-D02198561A90>

## Oldest record of a larva of long-legged velvet mite (Erythraeoidea) parasitising an immature planthopper

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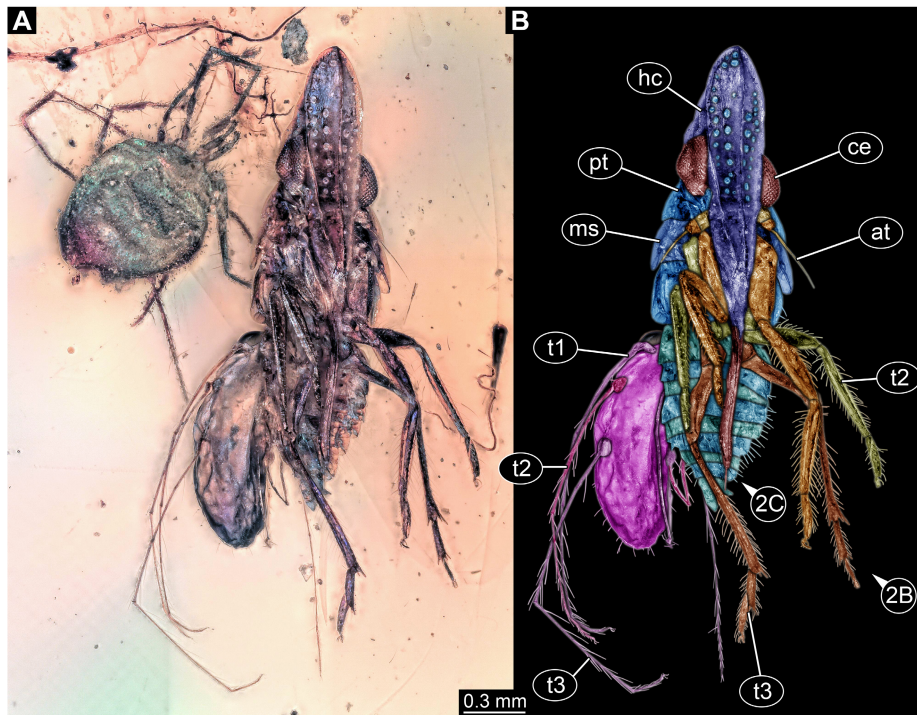
The fossilization of organisms in amber displaying the behaviour in which they were engaged when becoming entrapped in tree resin is known as “frozen behaviour” (Arillo, 2007). Findings of frozen behaviour are rare and can uncover valuable information on how food webs were structured in the past. One of the most reported interactions between organisms in amber is the case of parasitengonan mites still attached to their hosts (De Baets *et al.*, 2021). Parasitengona is an ingroup of Trombidiformes characterised by a complex life cycle (Krantz & Walter, 2009) in which the active post-larval forms (deutonymph and adult) are predatory, while the six-legged heteromorphic larva (for challenges of the term, see Haug, 2020) is parasitic on euarthropodan and vertebrate hosts (Małkol *et al.*, 2012). Given the firm grip of most parasitengonan mites to their hosts (*e.g.*, Åbro, 1988), these mites are often found in amber still attached to them (De Baets *et al.*, 2021). Among Parasitengona, there is an ingroup characterised by their extremely long legs (Wohltmann, 2000), Erythraeoidea, or long-legged velvet mites. Erythraeoidean larvae parasitise several euarthropodan groups, with few exceptions (Stroiński *et al.*, 2013). Most known hosts from the fossil record are dipterans (as reviewed by Arillo *et al.*, 2018; Arce *et al.*, 2024), with a few reports on other insects: a moth (Poinar *et al.*, 1991), a spider and a booklouse (Weitschat & Wichard 1998), and a cicada (Poinar *et al.*, 2012). Here we report a piece of Kachin (Myanmar) amber of *ca.* 100 Mya with a mite attached to a planthopper. We further discuss its implications for the host-parasite relationship of Erythraeoidea.

**Material and methods.** This study focuses on bioinclusions found in an amber piece from Kachin amber, Myanmar. The age of Kachin amber is of about 100 million years (Shi *et al.*, 2012). The specimen is part of the collection of one of the authors (PM) and is deposited under repository number BUB 3747.

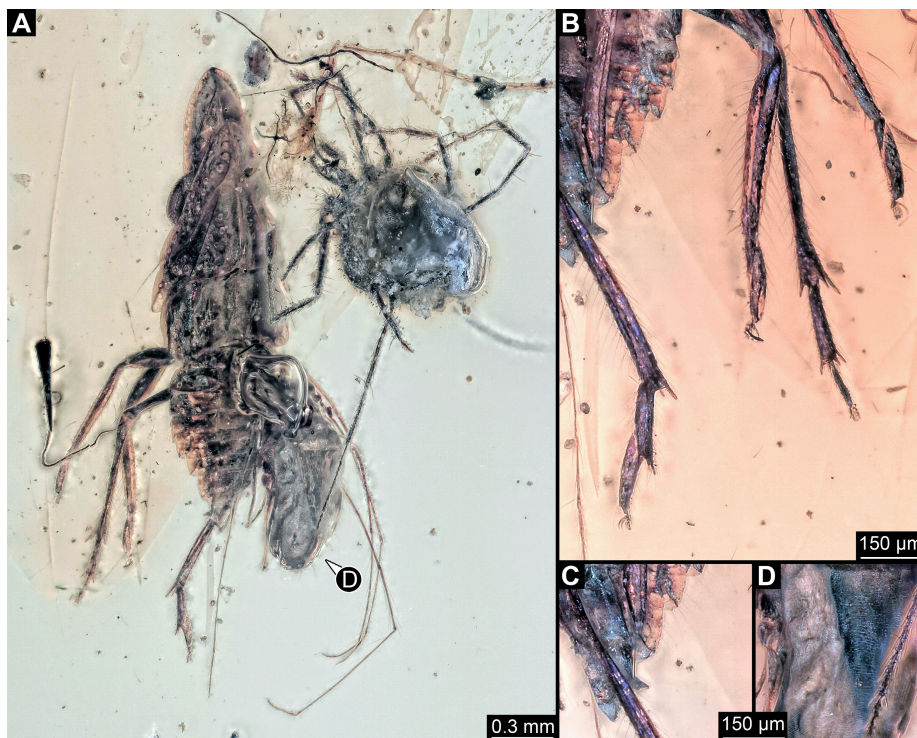
The bioinclusion was documented with the aid of a Keyence VHX-6000 digital microscope using different illumination settings, white and black background. We also applied the HDR (High Dynamic Range) function, which combines multiple frame captures using different exposures into a single photo. Images in x-y axis and adjacent frames were merged into a single panorama by the built-in software. The sharpest photos enhancing contrast, and showing the highest degree of detail, were then selected. Further processing was performed using Photoshop CS2.

**Results.** The syninclusion (Figs 1, 2) consists of a mite (mite A) and a planthopper in close contact through the anterior part of the mite feeding apparatus (gnathosoma) and the abdomen of the planthopper. Next to them is an additional mite (mite B).

Mite A: Body organised into gnathosoma (functional head) and idiosoma (trunk), most relevant characters accessible in the ventrolateral position (Fig. 1A). The surface of the cuticle on the idiosoma bears a pattern of ridges (Fig. 2D). Urstigmata (or Claparède’s organ; osmoregulatory organ) apparently absent. The mite has three pairs of legs (trunk appendages), therefore representing a larva. The three coxae (basipods) of the legs are distant from each other. The first pair of legs is 1.6 times the length of the idiosoma, the second pair of legs is 1.4 times the length of the idiosoma, and the third pair of legs is 1.7 times the length of the idiosoma. The mite seems to be attached to abdomen segment 2 of the planthopper via the anterior part of the mite feeding apparatus (gnathosoma), although the precise attachment area is not visible on either side of the amber piece: on one side the attachment site is blocked by the planthopper (Fig. 1A), and on the other side it is blocked by a bubble (Fig.



**FIGURE 1.** Long-legged velvet mite larva (ventrolateral view) attached to a planthopper (ventral view), and a post-larval parasitengonan mite next to them (dorsal view). **A**, Overview. **B**, Colour marked. Abbreviations: at = antenna; ce = compound eye; hc = head capsule; ms = mesothorax; pt = prothorax; t1–3 = trunk appendages (legs) 1–3; 2B = trunk appendage of the planthopper, details in Fig. 2; 2C = stylet of the planthopper, details in Fig. 2.



**FIGURE 2.** Long-legged velvet mite larva (dorsolateral view) attached to a planthopper (dorsal view), and a post-larval parasitengonan mite next to them (ventral view). **A**, Overview. **B**, Distal elements of the trunk appendages (legs) of the planthopper (from Fig. 1). **C**, Close-up on the distal part of the planthopper beak with extended stylet (from Fig. 1). **D**, Close-up of the surface of the idiosoma of the mite larva.

2A). The idiosoma (functional trunk region) shows some level of distension, indicating a possible case of engorgement.

Mite B: Most relevant characters of the specimen are accessible in dorsal view (Fig. 1A). Gnathosoma bearing slender

pedipalps. Armilla (extensible collar in the gnathosoma) absent. Idiosoma round, covered in numerous but separated setae. Aspidosoma (anterior area of the idiosoma) bearing a small nasus (prodorsal projection). Crista (dorsal median thickening of the idiosoma) and dorsal shield either absent or not visible. Four pairs of long legs, hence an active post-larval stage, bearing both short and elongated setae. Leg 1 longer than the rest of the legs. Leg 1 and 4 longer than the idiosoma. Femur sub-divided. Tibia 1 thicker than the rest of the leg and elongated. Tibia 2 thicker than the rest of the leg and shorter than in leg 1. Tibia 3 not visible. Tibia 4 almost as thick as the rest of the leg.

Planthopper: Body length about 2.2 mm. Eumetope (frons, frontal head sclerite) at each side with two longitudinal rows of sensory pits. At least half of the compound eyes concealed by pronotum from dorsal view. Beak long, extending to abdomen segment 8; stylet extended (Fig. 2C). Pronotum inverted V-shaped, median carina doubled, with two oblique longitudinal rows of sensory pits. Lateral carinae of mesonotum sharp, mesonotum with sensory pits in areas between median and lateral carina, paradiscal area, and forewing pad. Metanotum with faint laterodiscal carinae, clusters of sensory pits in discal area and hind wing pad. Fore and mid tibia somewhat foliaceous, with distinctive colouration. Hind tibia without lateral spine, with five visible asetigerous apical teeth. Hind tarsus with two elements (tarsomeres); tarsomere 1 apparently wider and longer than tarsomere 2, about 1.5×; tarsomere 1 with at least four seta-bearing teeth visible (Fig. 2B). Claws of hind leg small.

**Discussion.** The three pairs of legs on the mite attached to the planthopper are characteristic of mite larvae. The gnathosoma is not accessible since the mite is attached through it to the planthopper's abdomen and due to a bubble being present on one side of the amber piece. The dorsal shield is also not visible due to the position of the mite. The general body shape, the large distance between coxae 1 and 2, the apparent absence of urstigmata and the extremely long legs point to the mite being a representative of Erythraeoidea (Wohltmann, 2000). Additionally, the ridge pattern on the surface of the cuticle is similar to the ones depicted on other living specimens of erythraeoidean larvae (e.g., Southcott, 1961: figs 21, 22).

The mite with four pairs of legs is a post-larval mite, either a nymph stage or an adult. Unfortunately, relevant characters, such as chelicerae, the crista, dorsal shields, bothridia or the number of eyes (Krantz & Walter, 2009), are not visible in the specimen. The general body shape and setae disposition on idiosoma points to it being a representative of terrestrial Parasitengona. The specimen does not have sclerotised bands on dorsum of idiosoma, hence it is not a Trombellidae. The absence of an armilla (extensible collar in the gnathosoma) also rules out Smarididae (Southcott, 1961). Nevertheless, since most relevant characters for distinguishing parasitengonan ingroups are not visible, the mite can only be identified as a post-larval representative of Parasitengona.

The immature planthopper can be identified as a representative of Dorytocidae, which is an extinct group exclusively known from Cretaceous Myanmar amber, based on

the composition of its characteristics as follows: the inverted V-shaped pronotum with a doubled median pronotal carina, sensory pits present on the disc of meso- and metanotum, foliaceous fore and mid tibia, dorsum of abdomen carinate, and the absence of wax-pore plates (Emeljanov & Shcherbakov, 2018). Furthermore, the new fossil shares significant morphological similarities with the second post-embryonic stage of *Dorytocus ornithorhynchus* (Emeljanov & Shcherbakov, 2018), although its body is much shorter and the number of distal teeth on the hind tibia and tarsomere 1 differs.

The anterior part of the gnathosoma of the mite larva is very close to the abdomen of the immature planthopper and there is an apparent engorgement of the mite. These are both strong indications that the mite has been attached to and feeding on the planthopper when entrapped in the resin. However, since aberrations in the amber piece do not allow further resolution of the attachment site of the mite, we cannot exclude the possibility that the mite and the planthopper nymph are simply preserved very close to each other.

In the extant fauna, there are several records of a parasitic interaction between erythraeoidean larvae and hemipterans, including planthoppers (reviewed by Stroiński *et al.*, 2013). Although extant long-legged velvet mites are found parasitising a long list of different euarthropodan hosts (Stroiński *et al.*, 2013), most of the reports of parasitism by erythraeoideans in the fossil record are of dipteran hosts (see above). Poinar *et al.* (2012) found two long-legged velvet mites attached to another hemipteran, an adult cicada (*Minyscapheus dominicanus*), in Miocene Dominican amber. To the best of our knowledge, our present discovery constitutes the fifth record of a non-dipteran host in the fossil record, and the oldest record of a long-legged velvet mite attached to a hemipteran specimen.

In the case here reported, the hemipteran is immature. Immatures of Dorytocidae could have been living on bark (corticolous) in the Kachin amber forest, as indicated by morphological specialisations, such as the foliaceous fore and mid tibiae, the edges of the abdomen, the long beak, and cryptic colouration (Emeljanov & Shcherbakov, 2018; Amaral *et al.*, 2024). Unfortunately, most records in extant specimens do not mention the stage of the planthopper host, except for the ones reported by Małol *et al.* (2014) and Xu *et al.* (2020), in which both specimens appear to be adults, since their sex was reported. In fact, there is no known record in the present fauna of planthopper immatures being parasitised by erythraeoidean mites. However, there are records of erythraeoidean larvae parasitising other hemipteran immatures (Torrice-Bazoberry *et al.*, 2020). In the previously reported fossil record, the parasitised cicada is an adult (Poinar *et al.*, 2012).

In the present record, the mite was attached to the second segment of the abdomen of the planthopper. From the reported long-legged velvet mites on planthoppers in extant fauna, in the only record in which the place of attachment is reported, mites were also attached to the abdomen of its female host (Flatidae, Małol *et al.*, 2014). Attaching to the abdomen region of the host may help parasitic mites to avoid being forced to detach by the host.

For parasitengonan larvae, hosts not only serve as a mean of nutrition, but also as a way of dispersing (Wohltmann, 2000). Despite not being such strong dispersers as hosts capable of flight, an immature planthopper may still possess a high jumping ability. With their extremely long legs, erythraeoidean mites could freely move for long distances among environments such as brush piles, sticks, and leaves, like thread-legged bugs (Emesinae). Yet, attaching to an immature planthopper could be helpful for spreading, for example, from one plant to another. However, the presence of the large-sized parasitic mite is likely to affect its movement capability. In fact, sublethal infestations of erythraeoidean larvae have been shown to affect the ability of the homopteran hosts to escape predators (LaMunyon & Eisner, 1990). The lower movement ability of the host could have also influenced the entrapment of both the host and parasite in the tree resin, leading to later fossilisation.

### Acknowledgements

YF is thankful for the support from the Alexander von Humboldt Foundation. JTH is supported by the Volkswagen Foundation with a Lichtenberg Professorship. We thank all people providing free and open-source software.

### References

Åbro, A. (1988) The mode of attachment of mite larvae (*Leptus* spp.) to harvestmen (Opiliones). *Journal of Natural History*, 22 (1), 123–130.  
<https://doi.org/10.1080/00222938800770091>

Amaral, A.P., Stotzem, L., Haug, G.T., Haug, C. & Haug, J.T. (2024) Immature planthoppers had longer mouthparts 100 million years ago as exemplified by quantitative morphology (Hemiptera, Fulgoromorpha). *Spixiana*, 46 (2), 201–226.

Arce, S.I., Haug, C., Haug, J.T. & Amaral, A.P. (2024) Driven apart: fossil parasitic long-legged velvet mite larvae on gall midges represent a long lost parasitic association between mites and dipterans. *Palaeoentomology*, 7 (2), 254–264.  
<https://doi.org/10.11646/palaeoentomology.7.2.9>

Ariño, A. (2007) Paleoethology: Fossilized behaviours in amber. *Geologica Acta*, 5 (2), 159–166.  
<https://doi.org/10.1344/105.000000301>

Ariño, 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>

De Baets, K., Huntley, J., Klompmaker, 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, Switzerland, 1–50.  
[https://doi.org/10.1007/978-3-030-52233-9\\_1](https://doi.org/10.1007/978-3-030-52233-9_1)

Emeljanov, A.F. & Shcherbakov, D.E. (2018) The longest-nosed Mesozoic Fulgoroidea (Homoptera): a new family from mid-Cretaceous Burmese amber. *Far Eastern Entomologist*, 354, 1–14.  
<https://doi.org/10.25221/fee.354.1>

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>

Krantz, G.W. & Walter, D.E. (2009) *A manual of acarology*. 3<sup>rd</sup> ed. Texas Tech University Press, Lubbock, 807 pp.

LaMunyon, C. & Eisner, T. (1990) Effect of mite infestation on the anti-predator defenses of an insect. *Psyche: A Journal of Entomology*, 97, 31–41.  
<https://doi.org/10.1155/1990/70973>

Mąkol, J., Kłosińska, A. & Łaydanowicz, J. (2012) Host–parasite interactions within terrestrial Parasitengona (Acari, Trombidiformes, Prostigmata). *International Journal of Acarology*, 38 (1), 18–22.  
<https://doi.org/10.1080/01647954.2011.583276>

Mąkol, J., Moniuszko, H., Świerczewski, D. & Stroński, A. (2014) Planthopper (Hemiptera: Flatidae) parasitized by larval erythraeid mite (Trombidiformes: Erythraeidae)—A description of two new species from western Madagascar. *Journal of Insect Science*, 14 (1), 194.  
<https://doi.org/10.1093/jisesa/ieu056>

Poinar, G.O., 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., Kritsky, G. & Brown, A. (2012) *Minyscapheus dominicanus* n. gen., n. sp. (Hemiptera: Cicadidae), a fossil cicada in Dominican amber. *Historical Biology*, 24 (3), 329–333.  
<https://doi.org/10.1080/08912963.2011.635791>

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>

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>

Stroński, A., Felska, M. & Mąkol, 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>

Torrico-Bazoberry, D., Pinto, C.F., Davyt-Colo, J. & Niemeyer, H.M. (2020) Response to selected ecological parameters by *Leptus hringuri* Haitlinger, 2000 larvae (Trombidiformes: Erythraeidae) parasitizing treehoppers (Hemiptera: Membracidae) from Bolivia on two host-plant species. *International Journal of Acarology*, 46 (3), 174–179.  
<https://doi.org/10.1080/01647954.2020.1751280>

Weitschat, W. & Wichard, W. (1998) *Atlas der Pflanzen und Tiere im Baltischen Bernstein*. Verlag Dr Friedrich Pfeil, München, 256 pp.

Wohltmann, A. (2000) The evolution of life histories in Parasitengona (Acari: Prostigmata). *Acarologia*, 41 (1–2), 145–204.

Xu, S.Y., Yi, T.C., Guo, J.J. & Jin, D.C. (2020) Four new species of larval Callidosomatinae (Acari: Prostigmata: Erythraeidae) and a newly recorded genus *Iguatonina* from China with notes on generic concept. *Systematic and Applied Acarology*, 25 (2), 285–326.  
<https://doi.org/10.11158/saa.25.2.9>